

A NATURALISTIC MODEL OF CLASSIFICATION AND ITS RELEVANCE
TO SOME CONTROVERSIES IN BOTANICAL SYSTEMATICS, 1900-1950

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ABSTRACT

There is currently considerable controversy within philosophy over how a natural kind terms' extension is determined. Adherents to traditional theories of meaning argue that extension is determined by intensional properties which usually consist of identifying descriptions. Recently a new, essentialist alternative to these traditional accounts has been advocated; proponents of this view maintain that a terms' extension includes all objects which are essentially the same as a given paradigm instance of the terms' use.

In the present thesis it is argued that both description theories and essentialism describe not how classification must proceed but rather two alternative strategies for how a classification of natural kinds might be attempted. A terms' extension is not determined in advance by either identifying descriptions or hidden essential properties since stress on either of these is itself a choice. This claim is exemplified by using empirical material drawn from the recent (post 1900) history of a classificatory science, botanical systematics. By means of this evidence it is shown that both "descriptionist" and "essentialist" strategies of concept application have been (and still are) pursued by different groups of taxonomists.

One consequence of the position outlined above is that classifications are conventions and that they are evaluated instrumentally. The force of this argument is best illustrated by conceiving of classifications as part of a wider network of beliefs which are socially transmitted and sustained. Changes in networks are designed to further the interests to which a network is being put. It is argued here that the main kinds of interests which have been important in twentieth century systematics are 1) interests in technical prediction and control and 2) professional vested interests. An important aspect of both these kinds of interests is that they are normally considered to be "internal" to science. It follows that to understand scientific knowledge from a sociological perspective does not, of necessity, entail commitment to "external" explanations of scientific change.

DECLARATION

This thesis has been composed by myself and the research on which it is based was my own work.

A Glossary of Some Botanical Terms

- Allopolyploid A polyploid plant to which two different species have each contributed one or more sets of chromosomes.
- Allotetraploid (= amphidiploid) Allopolyploid which arises when an ordinary hybrid between two different species, containing a set of chromosomes from each parent, doubles its chromosome number. Allotetraploidy is a means of overcoming hybrid sterility.
- Amphimixis True sexual reproduction.
- Angiosperms Flowering plants.
- Apomixis Reproduction which has the superficial appearance of being sexual but which takes place without fertilization and/or meiosis.
- Autopolyploid Polyploid in which all the chromosomes come from the same species (and often the same individual).
- Cryptogams Plants without seeds or flowers. Includes algae, fungi, lichens, mosses and ferns.
- Phenetic (classification) A classification based on maximum overall similarity.
- Phylogenetic (= phyletic) classification A classification based on closeness of evolutionary descent.
- Polyphyletic (species) A species whose members have had a quite separate evolutionary history, not being descended from a common ancestor.
- Polyploid A plant with more than the normal, diploid (2x) number of chromosome sets. Most polyploids are tetraploid (4x) or hexaploid (6x).
- Propagule Any part of a plant capable of growing into a new organism e.g. spore, seed, gemma, cutting.
- Type Specimen The original herbarium specimen from which a plant species was named and described.

Introduction

The research presented in this dissertation is unusual in several respects. It is an attempt to formulate a model of classification which will serve as a framework for understanding controversy within the classificatory sciences. In fulfilling this objective I have drawn on material from two fields normally considered as unrelated: the philosophy of meaning and the sociology of science. Moreover, I have tried to synthesize these two fields not in any abstract way, but through the use of historical material drawn from the history of botanical systematics.

In the past scientific classification, and the classificatory sciences in general, have been neglected by historians and sociologists of modern science. It is surely a symptom of this that one of the best textbooks of the history of biology in the twentieth century (Allan 1975) has no chapter on developments in either taxonomy or ecology. The reasons for this are not hard to guess - for taxonomy today is not regarded as a major "growth area" in biology and it is a discipline in which there have not been the spectacular developments evident in, say, molecular biology or genetics.

However, there is a current revival of interest in classification in philosophy. Much of this new awareness that classification is a problematical subject stems from the uncertainty placed on the belief in an independent language of observation. Such a language, if it existed, would form a stable and unchanging base for the erection of scientific taxonomies. However, recent work in philosophy (e.g. Hesse 1958, Feyerabend 1962) has cast severe doubt on the notion that there is any fundamental difference between "observational" and "theoretical" predicates in science.

Further, there has been a revived interest in the social sciences in classification. In social anthropology, where the knowledge under discussion is that of "primitive" societies the study of the classification of natural kinds is routinely held to be illuminating in the information it can yield (for a review of this literature see Willis 1974). In another

area, ethnomethodologists, who have sought to bring attention to the unexamined basis of social action and discourse and to the unexamined background of tacit assumptions which underlie practical reasoning in everyday life have found it necessary to treat classification as a problematic activity. To take just one example from a rapidly expanding literature, Garfinkel has shown that in accounting for a social event such as death we have to "do work", to actively maintain boundaries of classification. There are, according to Garfinkel, no rules which determine what final form these taxonomies take. Rather those "rules" are generated in the activity of classification itself (Garfinkel 1967: 14). For these reasons then, a re-appraisal of the nature of scientific classification seems particularly appropriate at the present time.

Chapter one sets the scene for what follows, through an examination of contemporary views concerning the nature of scientific taxonomies within science itself. As is shown in Chapter one, there is no agreement on the systematical principles which should underlie scientific taxonomy. On the contrary, modern systematics is an area where there is little agreement over methods, or even underlying objectives. In Chapter one I have set out to examine the broad divisions within current systematics, both at the level of theory and of methodology. Of particular importance is the distinction between classifications which are based on morphological description (orthodox taxonomy) and those based on genetical and cytological experimentation (biosystematics). Later chapters will enlarge on this division and its significance.

The lack of consensus within modern plant systematics is itself revealing. It suggests that if there are set rules for determining a classification of natural kinds then these rules have certainly not yet been "found" by all taxonomists. However, there is a further objective to Chapter one. It represents my own knowledge of taxonomy before I began the studies that led to the present dissertation. Naturally, in interpreting the historical material presented in later chapters I have attempted to set aside any prejudices this training gave and to display the views of earlier botanists within the framework

of their own historical epoch. However, if I have only partly succeeded in this exercise (and perhaps partial success is all that can be hoped for) then Chapter one reveals the likely sources of bias in my historical treatment.

Chapter two goes on to consider current theories about the nature of classification within philosophy. There is currently great division within the philosophical community over the question of how a terms extension is determined. According to traditional accounts of meaning, as exemplified by Copi (1972) and, in a modified form, by Searle (1953) a terms extension is determined by intensional properties consisting of identifying descriptions. Recently however a new account of extension has emerged which sees the extension of a term as including objects which are essentially the same as given paradigm instances of the terms use. This essentialist alternative to description theory is especially associated with the writings of Hilary Putnam. However, in Chapter two it is argued that both description theories and essentialism, contrary to their adherents claims, describe only how a classification of natural kinds might be constructed. It is argued in Chapter two that a point of philosophical importance follows from this, namely that the extension of a natural kind term is not given in advance by either identifying descriptions or hidden essential properties, since stress on either of these is itself a choice. The position taken in this thesis is that classifications are conventions and that a naturalistic model of classification must allow for this. This is best done by considering our taxonomies as part of a wider network of knowledge. Changes in classification can then be seen as options designed to further the objectives behind a given network. What these objectives have been in botanical systematics is not discussed in Chapter two, but is a topic reserved for discussion after the empirical material presented in Chapters three, four and five.

Chapter three deals with the earliest attempts to introduce experimental methods into taxonomy. The period of time covered in this chapter falls roughly within the two decades from 1900 to 1920. The major scientists whose work is discussed were geneticists, of whom

Alexis Jordan, Hugo de Vries and Jan P. Lotsy were of especial importance. As is shown in Chapter three the earliest attempts to experimentalise taxonomic procedures were promoted by scientists anxious to solve problems concerning the mechanism of speciation in plants and the apparently simple question: what is a species? A particularly interesting facet of these researchers is that they sought to locate the essence of a species in its hidden genetic microstructure. Ultimately these essentialist strategies of classification proved unsuccessful. The reasons for this failure lay outside taxonomy itself, in the increasing success of selectionist theories of speciation in the work of later geneticists and plant breeders.

The period from 1920 to 1930 saw fresh attempts to experimentalise taxonomy, mainly by ecologists. Chapter four investigates the reasons for this shift and concentrates especially on the work of the American botanist F.E. Clements and the Swedish botanist G. Turesson. Clements' work is of interest because it represents an approach to the problems of species classification and speciation which was radically anti-essentialist. Turesson's work is of significance because his genecological terminology used essentialist and descriptionist strategies of classification within a single system. This decade also saw an end to the debates over the mechanism of speciation. By 1930 the selectionist theories championed by the genecologists had triumphed, opening the way for the "neo-Darwinian synthesis" of the 1930's and 40's.

In the period since 1930 the approaches of experimental taxonomists to classification became much more diversified. There was a resurgence of interest in the use of genetical and cytological criteria in taxonomy, especially as applied at and below the level of the species. However, other experimentalists came to question the value of trying to incorporate experimental information about species into any system of categories. A third trend discernible in this period is the emergence of combinational strategies of classification. Combinational strategies, as their name implies, involve an approach to classification which is neither descriptionist or essentialist but which combines elements of both these strategies. These various diverse trends within experimental taxonomy after 1930 are described at length in Chapter five.

Chapter six returns to the problems posed at the end of Chapter two, namely those of considering what kinds of goals and objectives have structured and informed the classification strategies pursued by different groups of taxonomists since 1900. Drawing on the empirical material of the previous three chapters it is argued that the concept of "different interests in technical prediction and control" is of value both in explaining the rise of experimental systematics and in accounting for the resistance to experimental methods encountered in the writings of orthodox taxonomists. The different classifications of orthodox and experimental taxonomists are conventions designed to further different technical interests. As such they are designed to emphasise different aspects of reality and a choice between them cannot be made by an appeal to what is "natural" or "objective" or "really out there in reality". Indeed this conventional aspect of classification applies with equal force to theories about speciation, as is shown in Chapter six.

Finally, it is argued that different strategies towards classification cannot be explained in terms of technical interests or objectives alone. Vested professional interests and ideological concerns have also shaped the classification strategies adopted by twentieth century taxonomists. The role of these kinds of interest are discussed in Chapter seven.

An important theme running through both chapters six and seven is that technical and professional interests (which appear to have been the major influences on twentieth century plant systematics) are internal to science. They constitute what Kuhn (1971: 304) calls, "the internalities that shape the development of any discipline". A sociological approach to scientific knowledge and growth does not necessarily entail "external" history of science. Both "internal" and "external" factors can effect the development of scientific cognition and to ignore either is to place in jeopardy a full understanding of the cultural phenomenon called science.

A note on Historical Sources

Very little historical work has been done on twentieth century systematics. In the historical material presented in chapters three, four and five I have relied in the main upon published, primary sources. However, in discussing the wider context of twentieth century biology in which these developments in taxonomy were taking place I have relied quite extensively on secondary historical accounts and especially on the writings of Garland Allen (genetics), William Provine (Population genetics), Mark Adams (Russian Population genetics) and Ernst Mayr (evolution theory).

The historical chapters in the thesis are intended primarily to illustrate the theoretical discussions about classification presented in chapters one, two, six and seven. As "pure" history they are deficient in several respects. I have concentrated almost exclusively on taxonomy in English speaking countries or taxonomists, like Turesson, who published most of their research in English. Also, although the intellectual aspects of taxonomy are discussed in some depth no detailed attempt is made at an institutional history of taxonomy during the period covered by the text. Studies to rectify these lacunae are badly needed and hopefully the realisation of the theoretical interest of classificatory sciences to sociologists and philosophers will stimulate more research in this area. If the present thesis helps such a development then it will have fulfilled one of its major objectives.

Chapter One: The Nature of Scientific Classification part one:

Some theories of classification current in plant systematics

The object of the present chapter is to look at theories about the nature of scientific classification which are current in plant systematics. However, before discussing theory it will be necessary to examine the aims and methods of taxonomical research. General textbooks of plant systematics (e.g. Davis and Heywood 1963, Heywood 1967) divide plant taxonomy itself into four major fields: orthodox or morpho-geographical taxonomy, experimental taxonomy or biosystematics, numerical taxonomy and chemotaxonomy. We may thus begin by briefly considering the aims and methods of each of these research traditions within plant systematics.

1. Orthodox taxonomy. According to Davis and Heywood (1963: 2), modern taxonomic research, regardless of the methods employed, has three basic underlying objectives:

a. To provide a convenient method for identification and communication of information about the organisms which have been classified.

b. To provide a classification which expresses natural relationships in the plant world.¹

c. To detect evolution at work, discovering its processes and interpreting its results.

However, which of these aims is the most important and whether they are in fact compatible aims for any one system of classification to achieve are issues which divide the taxonomic community. Orthodox taxonomists, in general, have denied that it is possible or desirable

1. The term "natural" as used in current systematics has at least two distinct meanings. On the one hand it can mean a classification based upon overall resemblances. In this sense a natural classification uses properties from all parts of the plant - root, stem, leaves etc., as opposed to an artificial classification which might just be based on, for example, the characters of the flower or fruit. However, a natural classification can also mean a classification which is based upon evolutionary relationships. Thus, both phylogeneticists and pheneticists see their classifications as "natural".

that any single classification should encompass all of these objectives. A classification which always reflects evolutionary processes is deemed to be incompatible with the needs of a classification designed for identification and communication. As Davis and Heywood put it:

Classification should not be inconsistent with what evolutionary evidence is known, although there may be instances where it may be more convenient and serve more purposes if it is ... We hold the view that more than one kind of classification is possible and acceptable, and that no one can be judged best for all purposes.

(Davis and Heywood 1963: xviii)

Thus, the major aim of orthodox or 'classical' taxonomy is "to describe all existing kinds of plants, to classify them according to their resemblances and differences, and to name them according to a body of internationally agreed rules" (Heslop-Harrison 1953: 109). The 'rules' referred to are those pertaining to nomenclature. These were originally formulated at the First Botanical International Congress in Paris in 1867 and have been the subject of much amendment and discussion ever since.² Briefly, these rules lay down conventions concerning the naming of plant taxa. In the modern code the ranks or hierarchy of categories which can be legitimately used in the naming of a plant are as shown in Table 1.1. The code also deals with questions of priority concerning the naming of plants. A species binomial is not valid unless it is accompanied by a description, in Latin, of the characteristic properties of the new species. Also, where a plant has been named more than once it is normally the first name which is valid, although there are in fact many exceptions to this rule. It is another rule of the code that all individual plants belong to a species. The categories of the code are mutually exclusive; a given individual can only belong to one family, one genus, one variety, etc.

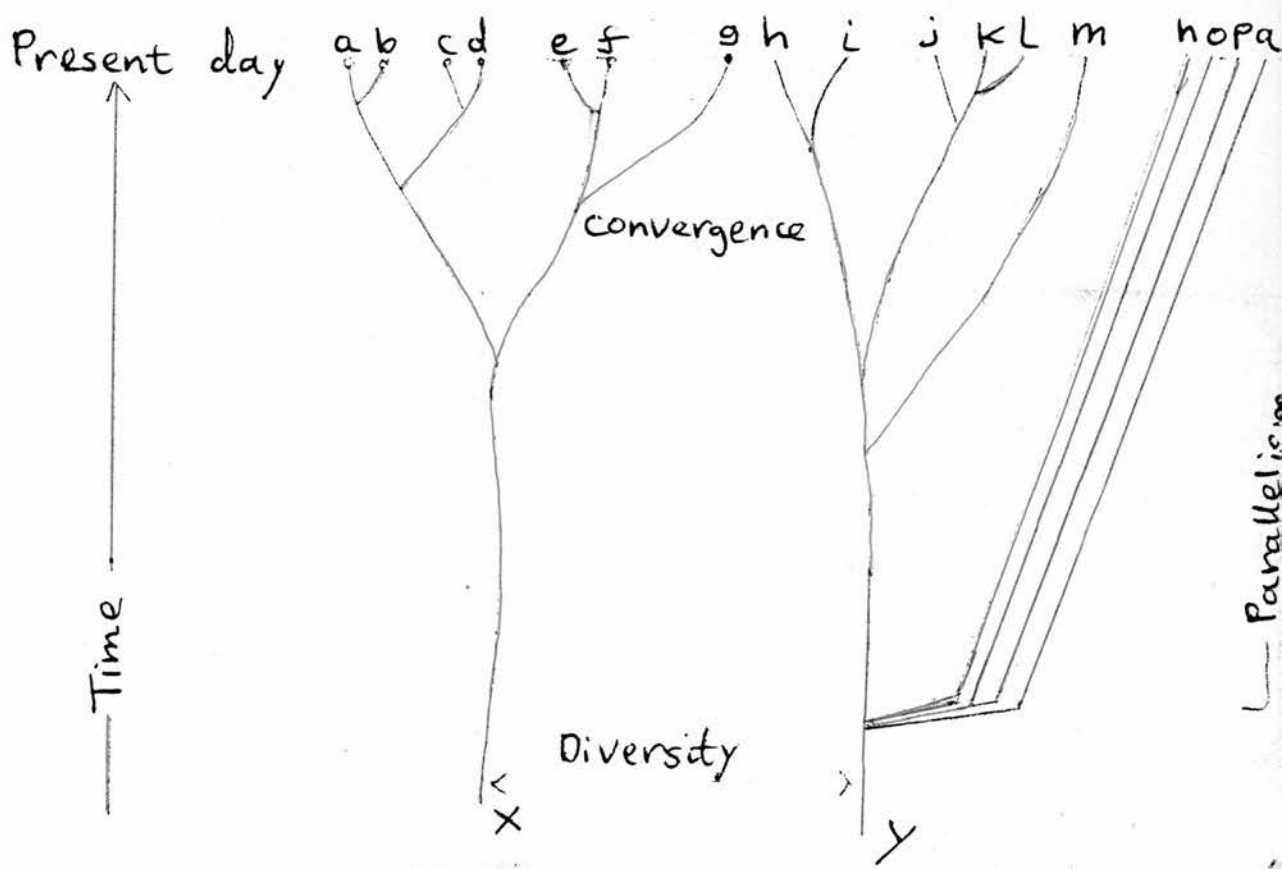
2. So far as we are aware, no historical work has been done on nomenclatural aspects of taxonomy in the period from 1867 onwards. Such a study would be of great interest, but cannot be undertaken here. For an elementary textbook on nomenclatural aspects of plant and animal taxonomy see Savory (1962).

Table 1.1. Ranks recognized in Current Botanical Nomenclature

Above the Species	Below the Species
Division	Species
Class	Variety
Order	form
Family	
Tribe	
Genus	
Section	
Series	

N.B. Where more ranks are needed the prefix "sub-" may be used in conjunction with any of the above terms.

Figure 1.1. Diagram illustrating Convergence and Parallelism (from Heywood 1967:19).



Orthodox taxonomy is typically a non-experimental or descriptive science. The emphasis in this kind of taxonomy is placed on the examination of the visible (i.e. external) morphological characters of the plant which, it is argued, provide the easiest and most convenient properties for classification. It is also the oldest of the research traditions within taxonomy. According to Heywood (1967: 3) the morpho-geographical approach to classification had its culmination towards the end of the nineteenth century, although he adds that it remains an important component of current taxonomical research.

Orthodox taxonomy is centred in, and dependent upon, the herbarium as an institution of taxonomic plant research.³ The herbarium is itself comprised of a large collection of dead plant material, dried and preserved on herbarium sheets and ordered according to some pre-arranged system of plant families.⁴ The herbarium is a very old institution: there were herbaria in existence prior to the time of Linnaeus.⁵ Most herbaria began as the private collection of an individual, but in later times herbaria have become adjuncts of other institutions concerned with botanical research, e.g. many of the larger university departments of botany have herbaria. In Britain the three main herbaria are government controlled and financed as part of the scientific civil service. These national herbaria are located at Kew, in the British Museum of Natural History in South Kensington and in Edinburgh. Kew, which is the largest, houses a collection of some $6\frac{1}{2}$ million specimens (Davis and Heywood 1963: 261).

Much of the day-to-day activities of the herbarium are concerned with the maintenance and preservation of this large collection of

-
3. For some empirical data supporting this position see later in this chapter and also Crowson (1970: 281-291).
 4. In British herbaria the arrangement of plant families is usually taken from Bentham and Hooker (1862-83).
 5. Very little historical work of a general nature has been done on the history of herbaria as scientific institutions. For an account of their modern role in plant systematics see McNeill (1968).

plant material. New specimens coming into the herbarium must be mounted, identified and "laid into" (i.e. added to) the existing collection. The collection provides a reference system for new and unknown plant material so that herbaria undertake routine identification services for other institutions such as medical services and the police.

Actual research within the herbarium will generally fall within one of two categories, viz. the production of floras and the preparation of monographs. Floras are lists of the plant species (with descriptions) of a particular area arranged in families and genera, together with keys to aid in their identification. Because the flora's primary function is to aid in the identification of plants, they usually contain little or no information of an experimental kind.

Monographs are fairly detailed revisions of a particular plant group (usually a genus). In modern monographs the importance of including biosystematical and experimental data where available is recognised and guidelines on the kind of biosystematical data which monographs should ideally contain were laid down at the Eighth Botanical International Congress in Paris in 1954.⁶ Sometimes new experimental work may be undertaken as part of a monograph's revision; Babcock's (1947) monograph on Crepis is an example of a monograph of this kind. In other cases the author of a monograph may simply review the existing literature on experimental work for the group under study. Monographs, therefore, represent one area of research output where orthodox and experimental taxonomy tend to become combined.

2. Experimental Taxonomy. The first two decades of the twentieth century saw rapid developments within the fields of plant cytology and genetics. The application of information drawn from these fields

6. G.L. Stebbins was the figure largely responsible for introducing these guidelines. A discussion of the Content of his proposals is given in Davis and Heywood (1963: 455-456).

to taxonomical problems resulted in the 1920's in the birth of the new discipline of experimental taxonomy or biosystematics. According to Heywood this new research tradition "replaced to a large extent conventional taxonomic approaches, especially in the universities" (Heywood 1967: 4).

In contrast to orthodox taxonomists, experimentalists have strongly emphasised the importance of basing classification upon evolutionary and genetic criteria. As V. Grant puts it:

A system of classification of the biological species must be judged, not on the basis of convenience, but according to whether it represents accurately or inaccurately the realities of nature.

(Grant 1957: 58)

In general experimental taxonomists have seen their aims as two-fold, involving firstly a new kind of approach to classification which will eventually replace orthodox taxonomy and secondly the setting up of a discipline whose function is to examine the nature of the evolutionary processes of plant speciation (cf. Davis and Heywood 1963: 451-452). However, in the more recent period (since 1935), some experimentalists have questioned the compatibility of these two goals. This tension within experimental taxonomy will be dealt with more fully in later chapters.

The methods of experimental taxonomy are diverse and drawn from a wide field of related disciplines, ranging from cytology, cytogenetics and genetics through to ecology and physiology. Amongst the most important tasks likely to be undertaken by the experimental taxonomist are: studies of chromosome number and its distribution in the species under study; standard transplantations of related forms into a uniform environment in order to assess the importance of hereditary and environmental factors on the plants' growth; and breeding tests to study the fertility of related populations. The field and laboratory, rather than the herbarium and library, are the centres of such investigations.

3. Numerical Taxonomy. Experimental taxonomy (or biosystematics) was a product of research begun in the 1920's. Numerical taxonomy is much more recent in origin, being a product of research carried out

mainly in the U.S. during the 1960's. The term "numerical taxonomy" implies more than simply the use of numerical methods and computers. The starting point of numerical taxonomy is the claim that neural estimates of resemblance are imprecise and subjective in comparison with proper statistical techniques (Sneath 1961: 98). The computer is used to ensure an equal weighting of characters and to prevent subjective weighting of one character over another. Because it was a tenet of the French philosopher Michel Adanson (1727-1806) that a natural classification is one which gives equal weight to all characters, numerical taxonomists have referred to their position as neo-Adansonian taxonomy (Adanson 1757, 1763; Sneath 1962).

Equal character-weighting means that classifications do not always reflect phylogenetic relationships or boundaries of gene-exchange, a fact which has caused controversy between numerical taxonomists and proponents of evolutionary taxonomy (for an account of this controversy see Ruse 1973: 154-173). A second consequence of numerical taxonomy is that it often results in the formation of taxa which are polythetic. Numerical taxonomists have defined such taxa as ones in which "no single attribute is in theory sufficient and necessary for membership in the group so long as the members share a high proportion of characters" (Sneath and Sokal 1962: 856). This also is a controversial aspect of numerical techniques for, at the species level especially, the existence of polythetic taxa means that the task of constructing workable keys for identifying specimens becomes extremely difficult. A brief account of significance of numerical taxonomy to general philosophical issues concerning the nature of scientific classification is given in Appendix A.

4. Chemotaxonomy. A fourth research tradition which has become increasingly important within plant taxonomy since the 1960's is chemotaxonomy or biochemical biosystematics. Chemotaxonomy has been especially useful in examining hybrids - the outstanding example being the work of Alston and Turner (1959) on Baptisia. In the long run the most exciting possibility opened up by chemotaxonomy is that it may allow direct estimates of genetic similarity by means of

techniques of DNA - hybridization.⁷ However, many orthodox taxonomists have opposed the argument that chemical characters are somehow more basic or primary to classification than, say, morphological or anatomical characters (cf. Davis and Heywood 1963: 222-258).

The separation of orthodox taxonomy from the new approaches of biosystematics, numerical taxonomy and chemotaxonomy is not meant to imply that, on occasions, taxonomists may not deploy techniques taken from several of these fields in combination. Davis and Heywood in their account of the relationships between orthodox taxonomy and biosystematics argue that it is a mistake to stress too highly the independence of these fields:

We have gone into the relationships between orthodox taxonomy and the newer (experimental) disciplines at some length since there are widespread misunderstandings as to their relative roles - an unhealthy situation for the progress of our science. Perhaps the greatest misunderstanding stems from the idea of separation between the two approaches. The separation is not between taxonomists and experimentalists but between some of their activities. Often the same botanists are engaged in both.

(Davis and Heywood 1963: 458, underlinings in the original)

The extent to which herbarium taxonomists employ experimental and quantitative techniques is a question which was investigated during an early phase of the present investigations. To this end a questionnaire was sent to the 82 taxonomists who are currently engaged in research at the three government herbaria in

7. Nucleic acids can form molecular hybrids by base-pairing. The long-term value of such techniques is that they make possible a classification based directly upon genotypic (as opposed to phenotypic) resemblances. However, some of the early work applying this technique to plant taxa has yielded highly anomalous results in terms of comparisons with established classifications for the groups in question (cf. Hoyer, McCarthy and Bolt 1964; Heywood 1967: 39-40).

Britain.⁸ As a part of this questionnaire the scientists were asked to record those research activities in which they were involved during an average working week. The responses to this question for the 53 replies which were received are shown in Table 1.2. In Table 1.2 activities 1 to 14 correspond to what is normally regarded as "orthodox" taxonomical methods. Activities 15 to 21 all involve experimental and numerical techniques which are usually considered to be part of the "new" systematics in the broadest sense. The results of this study can only be considered as very tentative. There is no information on the work going on in regional or local herbaria, or of the type of taxonomical research being undertaken in the universities. However, what information there is suggests that, in the major herbaria at any rate, there has been little move towards the adoption of numerical and experimental techniques.

The persistence of orthodox taxonomy side-by-side with the new approaches of biosystematics, chemotaxonomy and numerical taxonomy is also evident from the debates which are currently engaging taxonomists concerning theoretical issues within systematics. The diversity of methods in modern taxonomical research is reflected in these discussions.

Theoretical issues in modern plant systematics

The discussion below will be divided into four sections. Section one deals with the distinction between phylogenetic and phenetic theories of classification. Sections two and three examine current controversies concerning the way in which species could be defined and the problems concerned with the classification of intra-specific units. Finally section four deals with typological theories of variation and their distinction from populationist approaches to the study of variation.

8. The list of taxonomists working in these three herbaria was obtained by writing directly to the heads of the institutions concerned. We would like to take this opportunity to express our thanks to the staff of these herbaria for their help in replying to the questionnaire which was sent to them.

Table 1.2. Activities of 53 scientists in the 3 Government herbaria in Britain.

	Activity	A	B	C	D
1	Library work	20	12	11	8
2	Nomenclatural studies	22	12	9	7
3	Identification of Plants	25	7	9	7
4	Laying in specimens	6	3	2	2
5	Preparation of materials for distribution	5	N.D.	N.D.	18
6	Curation of collections	15	N.D.	N.D.	50
7	Dealing with loans of specimens	12	N.D.	N.D.	4
8	Formulation of keys	21	N.D.	N.D.	7
9	Studying morphological characters using dried herbarium material	24	11	12	8
10	Studying morphological characters using living material	13	2	9	4
11	writing plant descriptions	21	N.D.	N.D.	7
12	Studying Plant distribution and geography	23	9	8	7
13	Studying micromorphological characters using the light microscope.	18	11	10	74
14	Studying micromorphological characters with the electron microscope	4	3	—	13
15	Studying Anatomical characters with the light microscope	5	7	2	26
16	Studying Anatomical characters with the electron microscope	2	3	1	11
17	Large scale studies of Plant populations using statistical techniques	—	—	—	0
18	Studying cytological characters	—	2	2	8
19	Studying genetical characters	—	1	1	4
20	Studying biochemical or physiological characters	—	2	2	8
21	Doing computer studies (Numerical taxonomy)	2	1	—	6
	other Activities	11	1	4	30

Key : A = Kew, B = London, C = Edinburgh

D = % of scientists who engaged the activity

N.D. = No Data.

1. Phylogenetic and phenetic theories of classification

A phylogenetic classification may be defined as a classification which is based upon closeness of evolutionary descent. A phenetic classification is one which is based upon maximum observable similarity.

In practice phenetic and phylogenetic classifications are often identical because similarities between organisms are usually the result of evolution from a common ancestral population. However, this is not always the case because of the phenomena of convergence and parallelism. Parallelism is defined as "the development of similar features separately in two or more, genetically similar, fairly closely related lineages" (Heywood 1967: 18). Convergence is "the development of similar features separately in two or more genetically diverse and not closely related lineages and not due to a common ancestry" (Heywood 1967: 19). These terms are illustrated in Figure 1.1. As a result of convergence and parallelism a phenetic classification does not always provide an accurate reflection of phylogenetic descent.

Both phylogenetic and phenetic theories of classification are very old and pre-date the rise of experimental taxonomy. The claim that classification should be based upon maximal numbers of characters is often traced back to the work of the French botanist Adanson.⁹ The assumption that classification could reflect phylogeny was prevalent after the acceptance of evolution in the latter half of the nineteenth century and since that time a number of phylogenetic

9. The claim that modern numerical taxonomy is "neo-Adansonian" is one which numerical taxonomists themselves make. From a historical perspective such a claim is dubious. Pratt (1977) has argued that Adanson had a very different concept of overall resemblance to that deployed by modern phenetic taxonomists. Thus, for Adanson, the number of "characters" possessed by a plant was finite and what constituted a character was laid down in advance. For the modern taxonomist this is not true.

classifications have been attempted for the angiosperms.¹⁰ However, although phylogeny is an older concept than experimental taxonomy, the rise of the latter in the 1920's and 30's was often seen as providing the pathway to a genuinely phylogenetic approach to classification (cf. Turrill 1939, and also Bennet 1964). However, the acceptance of phylogenetic principles is by no means universal. In their recent textbook Davis and Heywood argue that "the whole conception of phylogenetic classification is, we believe, a mistake except around the species level in favourable and well studied groups; and even there phyletic relationship often conflicts with genetic relationship as expressed by phenotypic resemblances" (1963: xviii). And, in taking this line, Davis and Heywood have received support from numerical taxonomists such as Sokal and Sneath (1963).

An issue which is closely related to the question of the relative merits of phylogenetic and phenetic principles of classification is that of character weighting. Character weighting may be defined as the giving of greater or lesser importance to one character over another in the production of a classification. Since the number of "characters" which can be employed to separate one species from another is potentially infinite, some character weighting is considered inevitable. Indeed, as Davis and Heywood (1963: 110-141) correctly maintain, the concept of what constitutes a "character" is itself problematical:

... the concept of characters as recognisable, separate entities is a product of man's necessity to communicate and therefore to describe. This explains why characters are so difficult to define.

(Davis and Heywood 1963: 110)

10. Although these different schemes have diverged widely in their details there is now general agreement that the Ranales (buttercups and magnolias) are the most primitive angiosperms and that the monocotyledons (grasses, etc.) were derived from the dicotyledons. The most recent attempts at a phylogenetic treatment of the angiosperms are those of Cronquist (1957) and Takhtajan (1958).

However, although selective weighting is an inevitable process which is not even avoidable in numerical taxonomy, phenetic taxonomists have maintained that characters should not be weighted on the basis of phylogenetic considerations. For example it was, according to Heywood (1967: 41), an assumption amongst many taxonomists that floral characters are particularly good for revealing evolutionary relationships. Such a priori weighting is rejected by pheneticists - all characters initially selected should be equally weighed and treated as of equal value until shown otherwise. A problem of this approach is that even where it is adopted the taxonomist may unconsciously and subjectively weight characters in his initial assessment of the plants with which he is dealing. It is a major claim of numerical taxonomists that their techniques overcome this problem of subjective weighting and thus make possible a genuinely phenetic classification.

2. Controversies over the definition of the term species

Of all the units classified by taxonomists it is the species which are of greatest potential importance to other branches of biology. Theories of species and how they originate are central to evolutionary theory, genetics and cytogenetics. Ecologists and phytogeographers require species lists for the habitats or geographical area under study before serious ecological work can begin. For this reason it is perhaps not surprising that the question of how species should be classified and defined has been a source of continual controversy within systematics. The species problem "is, if nothing else, a problem" (Davis and Heywood 1963: 89).

In the past much of the controversy surrounding the term species involved a philosophical division between "nominalists" and "realists". Prior to the emergence of evolutionary doctrines species were widely held to have been created by God and to be immutable in form. As such they presented objective entities in nature whose existence was real. However, by the end of the nineteenth century, many biologists had concluded that species were abstractions and that in nature there

existed only the individual. For Bessey (1908: 218), "nature produces individuals and nothing more ... species have been invented in order that we may refer to great numbers of individuals collectively." One of the central tenets of the "new systematics" of the 1930's and 40's was the reaffirmation of the objectivity of the species; species were real because they were reflections of real barriers to gene-exchange in nature.

Although the debate between "nominalists" and "realists" still continues (cf. Mayr 1957: 6), the major controversies in recent discussions of the species problem have centred around finding the correct operational definition of the term "species". Attempts at species definitions of this sort can themselves be grouped into three kinds (cf. Meglitsch 1954):

1. Morphological or taxonomic species definitions.
2. Biological or genetic species definitions.
3. Evolutionary or phyletic species definitions.

The taxonomic or morphological species concept is very old, and the use of external morphology to classify species is perhaps the most intuitively obvious way of approaching the problem of classifying biological natural kinds. According to this perspective, species are assemblages of morphologically similar individuals separated from other such assemblages by morphological gaps. Linnaeus was, in an important sense, an advocate of this approach for in practice he both described and defined his species on morphological criteria and Species Plantarum forms the official starting point for modern botanical species nomenclature as recognised by the International Code. Two morphological definitions of the species employed in recent textbooks of botanical systematics are as follows:

(The species is) a community whose distinctive morphological characters are in the opinion of a competent systematist sufficiently definite to entitle it to a specific name.

(Regan, quoted in Savory 1962: 63)

(Species are) the smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotypes.

(Du Rietz, quoted in Davis and Heywood 1963: 92)

The recognition of species by morphological criteria has been one of the primary aims of orthodox taxonomy and the herbarium method is designed to facilitate such a task. Indeed, because the morphological species concept is so widely used by taxonomists, Davis and Heywood recommend that it should be termed the "taxonomic species concept" in recognition of its "overwhelming use by taxonomists as opposed to biosystematists, genecologists etc." (1963: 93).

Historically, the morphological species concept has often been linked to typological thinking, i.e. to the view that all members of a species are essentially the same and that, therefore, one individual can be taken as representative of the species. Linnaeus himself is the prime example of a taxonomist who held to this principle (cf Stafleu 1971: 25-31). However, it is not correct to assume that the use of a morphological species concept necessarily entails a commitment to typology. Certainly, if species were constant and if they were always separated by essential properties of identity from other species, then the morphological species concept becomes a very easy one to apply. However, the acceptance that individuals of a species are not constant, either in their phenotype or genotype has not led to an abandonment of the morphological species concept but rather to its refinement:

Taxonomists regard their specimens as samples of natural populations, not just herbarium samples. They base their decisions about specific delimitation on the presence or absence of morphological breaks in the variation shown by these populations... Population, as employed in this sense, means an assemblage of plants with a particular distribution: its paramaters are judged on morphological evidence.

(Davis and Heywood 1963: 92)

To summarise: adherents of morphological species concepts have sought to define species in terms of characters of populations which are "phenotypical" in the modern usage of that term, i.e. in terms of characters manifested by an organism rather than in terms of the set of genes possessed by it. For practical reasons external morphology has been the main source of such characters. In the past taxonomists have also held that some of these morphological characters are essential to a species, i.e. they are possessed by all members of

that species and they define the "essence" of that species. If such characters can be located, then a species can be described from a single specimen. However, a commitment of this kind to a "typological" or "essentialist" theory of variation not a necessary component of a morphological approach to the use of the term species.

A completely different way of defining the term species has been to stress reproductive or genetic criteria as the means of distinguishing one species from another.¹¹ Such a biological species concept is, like the morphological species concept, very old. Linnaeus, although he delimited species on the basis of morphological criteria, nonetheless also believed it to be a further property of species that they would breed true under cultivation (cf. Stafleu 1971: 89). Indeed, for Linnaeus this was one possible means of distinguishing species from varieties - the latter, he held, would not breed true in subsequent generations. Two modern biological definitions of the species are those given by Grant and Mayr:

Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.

(Mayr 1942: 120)

According to the biological species concept the species is a population set apart from the rest of the living world by reproductive isolating mechanisms.

(Grant 1957: 54)

Reproductive isolation is usually accompanied by distinctive morphological discontinuity. However, it has been one of the discoveries of biosystematics that this is by no means necessarily the case. On occasions populations with very distinct morphological differences may freely exchange genes. Alternatively, cases are also known of sibling species, i.e. populations which are good species in the biological sense but which are difficult or impossible to separate on the basis of morphological resemblance. For these and other reasons many taxonomists have denied that species in the

11. For examples of actual taxonomic groups where those different species definitions have been employed see later chapters, especially chapter 6.

biological sense can be always incorporated into a group's taxonomic treatment. The continued controversy over this issue is well illustrated by the following quotations from two recent text-books on plant systematics:

As long as the concept of morpho-species is allowed to remain unmodified, taxonomy is handicapped in its efforts to contribute to biological progress ...

(Savory 1962: 94)

To abandon the practical, almost universal use of the term species in a primarily morphological-geographical sense for orthodox classification in favour of a restricted usage for impractical, largely theoretical units in terms of gene-pools and reproductive barriers, would surely be short-sighted and unrealistic.

(Davis and Heywood 1963: 98)

It follows, then, that definitions of species in terms of morphological and genetical criteria do not always lead in practice to the discovery of the same units or natural kinds. The same is also true if the third type of species definition is employed - the phylogenetic or evolutionary species concept. A species definition of this kind is given by Simpson:

An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies.

(Simpson 1961: 153)

For proponents of the biological species concept this definition of the species has the advantage of covering those groups of organisms where, because the breeding cycle is not sexual, a biological species definition is inappropriate (cf. Grant 1971: 37-45). However, such a definition can only really be of service where a good fossil record exists and for this reason it is a concept of the species which has had little direct application in angiosperm taxonomy. This species concept has been most consistently advocated amongst zoological paleontologists working on groups with a good fossil record (cf. Burma 1949a, 1949b; Mayr 1949; Crowson 1970: 57-67).

Philosophers of biology sometimes seem prone to the misconception that the biological species concept and the evolutionary species concept are "logically" compatible with one another but not with the morphological species concept. Hull (1965: 2) talks of the biological

species concept as being an "operational" version of the evolutionary species concept. Similarly, Giray (1976: 322) has argued that "the gene pool concept of Mayr... and the evolutionary concept of Simpson are logically independent but nomically convergent."¹² For this reason it is perhaps worth stressing that biological and phylogenetical species definitions do not always lead to the same units being regarded as species. That they do not is because some species are polyphyletic. A species may be said to be polyphyletic when some of its members have had quite distinct evolutionary histories, not being descended from a common ancestor which is also a member of that group. An interesting example of a case where this kind of speciation appears to have taken place is the grass Poa annua (cf. Tutin 1957). There is now bio-systematic evidence that P. annua has arisen several times from independent populations of P. infirma and P. supina. Of course this could be taken as evidence that P. annua is really two or more species, but this would be in conflict with the biological and morphological criteria for defining species which were considered earlier. Some more examples of polyphyletic groupings are discussed in chapter 6.

In conclusion it is worth asking why there has been so much controversy surrounding the question of species definitions and why, as Simpson (1961: 149) puts it, "the problem ... has probably caused more ink to flow than any other point in taxonomy." Blackwelder (1967) argues that much of the problem derives from the failure to distinguish between the various meanings of the term species, and Mayr (1957: 12) argues that the "hidden reason for so much disagreement" is the continuing attempt to find a single definition for the term species that will unambiguously define its usage. Hull (1965) also places strong emphasis on this interpretation and argues that the search for a single non-disjunctive species definition is itself a manifestation of Aristotelian thinking in biology, i.e. it is a product of the search for a single "essence" which will define a term's use.

12. It is interesting that Giray and Hull found it necessary to lump together phylogenetic and biological species concepts in this manner. Presumably both species concepts are seen as in harmony with "good" science (one being based on evolutionary theory and the other on genetics), so both have to be defended against "bad" orthodox taxonomy which lacks a modern approach.

However, there is an alternative approach to the problem of why there is a species problem, an approach which emphasises the close link between species concepts and the everyday practices and concerns of morphological and experimental taxonomists. The fact that most species "definitions" are in fact little more than operational prescriptions for how species groupings can be made means that there is a particularly close link in this instance between theory and practice. The species problem is such a sensitive issue in taxonomy, not just because species are important theoretical units in evolutionary and taxonomic studies; it is mainly an issue of concern because preference for one species concept over another involves commitment to one of a number of different and potentially rival sets of practices and techniques. These methods are, in turn, linked to different bodies of professional expertise and alternative institutional locations. The battle for the species is, from this perspective, just one aspect of the wider issues of methodology which have confronted taxonomists during the course of the current century.

3. Controversies over classification below the level of the species

The nature of the species has been a cause of considerable controversy between orthodox and experimental taxonomists. However, this controversy has not been restricted to classification at this rank. There has also been considerable disagreement over what units should be applied below the level of the species.

Linnaeus originally provided for only a single rank below the level of the species, namely that of the variety. Further, Linnaeus held that varieties were due to accidents of cultivation and unworthy of the attention of serious botanists (Stafleu 1971: 63-66; Briggs and Walters 1969: 20-25). The modern International Code provides five categories below the level of the species, i.e. subspecies, variety, subvariety, form and subform. However, like the species itself, these units have mainly been used by orthodox taxonomists for morpho-geographical groupings. An example is the "subspecies". Most current herbarium taxonomists use the term subspecies to denote geographical races within the species whose morphological distinctness is not such as to permit specific delimitation (Davis and Heywood 1963: 98-100). Such units in evolutionary terms will often represent "incipient"

species and such morphological patterning is often a sign of partial reproductive isolation. However, subspecies can also be caused by the fusing of originally distinct species as a result of migration or the breakdown of ecological barriers.¹³ In phylogenetic terms the morpho-geographical "subspecies" of the taxonomist cover a number of different evolutionary situations. It was a major facet of the work of experimental taxonomists in the 1920's, 30's and 40's that they tried to find alternatives to the traditional taxonomic ranks employed below the level of the species.

4. Typological and population concepts in taxonomy

Taxonomy is a science which pre-dates the theory of evolution. Typological approaches to variation are in part a consequence of that fact. Typology may be defined as the view that all members of a taxa possess a common ground-plan or essence. In terms of its history as an idea, typological thinking in taxonomy can be traced back to the influence of the early Greek philosophers and in particular to Plato, Aristotle and Theophrastus (Hull 1965; Mayr 1976: 26-29). At the species level typological thinking also fitted well the Christian concept of species as fixed forms created by intelligent design.

The populationist approach to organisms denies that there are any common features which can constitute an essence or ground-plan for a species or for any other taxon. Instead, population thinking places great emphasis on the uniqueness of all phenomena in the organic world. According to Mayr (1959: 27) population thinking had its roots in Darwin's theory of evolution through natural selection, although it spread only slowly throughout biology during the latter half of the nineteenth century.¹⁴

13. The history of the two British 'species' of oak Quercus petraea and Q. robur illustrates this point. Originally found in different habitats and therefore rarely able to hybridize, human interference has meant that the two 'species' are now frequently found growing in the same woodland with hybridization and introgression a common result.

14. The claim that Darwin's work embodied a populationist approach to the study of variation is discussed in more detail by Egerton (1968) and (1970).

No modern taxonomist would deny that species evolve and that there is considerable intraspecific variation, both within the genotype and phenotype of the plant. However, recognition of this fact has not led to a complete abandonment of typological procedures and concepts, at any rate within orthodox taxonomy. Species are still named on the basis of a single specimen (the type) which is then employed as a standard reference for the correct application of that name. And it is at least arguable that a typological approach to variation is inevitable in most taxonomy:

It is quite true that the species and other taxonomic categories must today be considered as made up (ultimately) of populations, these should ideally be treated in terms of frequency distribution of the different variants of each character actually present at any time. It would be idle to pretend that more than a very limited amount of taxonomy can be practised in this way. In fact, taxonomists are inevitably forced to identify material by comparison with previously collected specimens, together with figures and descriptions, since the specimens used by the taxonomist are necessarily extracted from the population and only in very exceptional cases is he provided with (or can obtain) statistically adequate samples of the population. Thus every taxonomist builds up what one might call a typological picture based on his experience of each species ... It is a warranted and inevitable procedure and a justifiable extension of typology.

(Davis and Heywood 1963: 11)

The argument of Davis and Heywood is not a plea for a return to the typological views of, say, Linnaeus or John Ray. However, it does suggest that the differences between "typological" and "populationist" approaches to the study of natural variation have been over-emphasised. A normal species is composed of millions of individuals and the population is, moreover, changing literally from moment to moment. It is obvious that a systematist, either of the biosystematical kind or an orthodox taxonomist working with a large number of specimens in a big herbarium, is only going to be able to record a tiny fraction of the enormous variability inherent in such a grouping.

Conclusion

Let us summarise the major points which have been made in this chapter concerning the nature of current theories in plant systematics.

Broadly speaking, the major areas of agreement and disagreement are as follows:

1. There is general agreement that classification must rest upon the characteristics of the organisms in question. However, which characters should be considered most important (e.g., those of the phenotype or those of the genotype) for classificatory purposes is not a matter on which any degree of consensus has been achieved.

2. There is general agreement that character weighting in some form is inevitable. Even in numerical taxonomy characters have to be selected. However, the value of weighting characters because of their presumed phylogenetic or evolutionary importance is denied by adherents of phenetic theories of classification.

3. It is generally accepted that the notion of just what constitutes a "character" is difficult to define. This is a practical problem in numerical taxonomy where, because of the procedures adopted, characters have to be explicitly verbalised and coded in mathematical form.

4. Whether biological classifications can or should always reflect evolutionary lineages is not a matter on which any consensus has been reached.

5. Similarly, there is no consensus regarding the use of the natural kind term "species" and whether these groupings should be made using morphological, genetical and phylogenetical data as the primary criterion for species membership.

6. It is accepted by practically all taxonomists that species evolve and that, in principle at least, no two individuals of a species are ever exactly alike in either their genotype or phenotype.¹⁵ However, whether it follows from this that all forms of typological thinking and procedures can be removed from taxonomy seems unlikely.

15. The only exception here would be clones, which are alike in their genotype but have a different phenotype due entirely to environmental factors.

Chapter Two: The Nature of Scientific classification part two:

Some theories of classification current in the philosophy of meaning

The examination of the nature and history of a classificatory science like plant systematics inevitably raises questions concerning the general nature of scientific classification. In what way do classificatory sciences differ from theoretical sciences like physics? Are the classifications used in science produced in some way which makes them fundamentally different from the classifications used in everyday discourse or within social institutions which are not a part of science? Do scientific classifications fundamentally differ in their nature and purpose from the classification schema devised and utilised by primitive societies? Does the activity of classifying in these different contexts, i.e. the scientific, the non-scientific, the primitive, involve different methods or models of classification, or are these activities manifestations, in different contexts, of a single underlying process? What determines the shape or form a classification takes in any given instance? How, and why, do classifications change and are such changes themselves determined and inflexible, or contingent and flexible? These are the kinds of questions which are raised and their solution demands an approach which synthesises perspectives current in both philosophy, sociology and history of science.

In answering these questions it is necessary to begin with accounts of classification produced by philosophers, because it is from this source, i.e. the philosophy of science, philosophy of language and semantics, that nearly all existing theoretical work on classification derives. However, our own aims in constructing a theory of classification differ fundamentally from those of most philosophers. In order to avoid misunderstandings it is necessary to stress these differences of aim.

In what follows, an attempt will be made to construct a model of classification from a naturalistic perspective. That is, we shall be concerned not with how human beings should carry out classification but how they actually do collectively carry out such activities. The normative element explicit or implicit in much of the writing of

philosophers when they talk about classification is absent in the account below. Their theories about how classifications ideally should be made are adapted to a different end. With a naturalistic account of classification inconsistencies between the theory and actual instances of classification carried out by scientists or others are real problems. One cannot take refuge in the admonition that the practitioners concerned should have done something else. In addition, whether the scientists could have proceeded more wisely or rationally will be of no concern in appraising our theory of classification, whereas it would generally be relevant to a philosopher when appraising such a theory.

Fortunately, many philosophers who have tackled questions about scientific classification from an avowedly normative stance have, nonetheless, produced accounts which do yield valuable insights from a naturalistic perspective.¹ In the present chapter four such theories are discussed. Two, the simple description theory and the cluster description theory are linked to traditional philosophical doctrines of reference and meaning. The third has emerged from criticisms of those traditional doctrines by, amongst others, Saul Kripke, Hilary Putnam and Keith S. Donnellan. The final theory of classification discussed here had a slightly different origin, in the work on scientific metaphor and inference of Mary Hesse. Certain general and abstract arguments will be presented that demonstrate that one of these accounts, that stemming from Hesse's work, is preferable as the basis for a naturalistic account of classification. In following chapters this theme will be expounded more fully, using empirical material drawn from the history of botanical systematics, and certain consequences of the Hesse model will be more fully explored.

With these preliminary remarks in mind it will now be possible to examine the first and historically the oldest and most entrenched of the four accounts of classification to be discussed, the simple description theory.

1. There is an interesting parallel here with Kuhn's (1970) account of cultural change in science. Kuhn claims his work is normative, but its great value lies in its insights concerning the actual nature of scientific discourse. The claim to be normative is best ignored here and this is true also of Hesse's (1974) account of scientific classification and induction.

Simple Description Theory

According to simple description theory we assign objects to a class by virtue of the discernible properties or attributes which these objects possess. Stated in formal terms simple description theory asserts that a term T can only be correctly assigned to an object X in virtue of that object's objective properties of T-ness.

However, not all the properties of an object are necessary for its classification. Consider the natural kind term "mammal". The important features of a mammal are its possession of hair, milk glands and young which are born alive. These are the characters which distinguish or differentiate a mammal from other natural kinds e.g. reptiles and birds, with which a mammal might get confused.

Thus, there is a distinction in traditional philosophical theories of classification between properties or attributes which are essential and those which are accidental.² Essential properties are those which any object must possess to be a member of that natural kind. They provide the criteria for separating members of closely related natural kinds. Accidental properties, in contrast, may be found in some members of the class but are non-essential for class-membership. Presence or absence of a tail would be an example of an accidental attribute for the natural kind term "mammal".

In practice the essential properties of animals and plants were usually sought for in easily visible aspects of the organism such as external morphology and behavioural attributes. We can thus speak of essential properties as making up an identifying description for the natural kind in question.

Taken together, the conjunction of essential properties provide a definition which governs a natural kind terms use. To put this another way, once we know the essential properties of a natural kind then we know how to determine the extension of that natural kind.

2. According to Brown (1968: 10) this distinction was first made by Aristotle.

Mammals are just those animals with hair, milk-glands and live-bearing young. The extension follows automatically once the identifying description is known:

identifying description
(= conjunction of essential —————> Extension
properties)

And a classification theory of this sort has categories which are mutually exclusive. For any object, X, X is either "mammal" or "not mammal". Mammals will all possess certain essential properties common to all members of the class; things which are not mammals will lack one or more of these properties.

Now this view of classification, or something very like it, is one which is associated with traditional philosophical accounts of meaning. The traditional account of meaning in philosophy holds that to know the meaning of a term is to know its intension and that to know the latter allows the extension of the term to be determined:

To understand a term is to know how to apply it correctly, but for this it is not necessary to know all of the objects to which it may be correctly applied. It is required only that we have a criterion for deciding of any given object whether it falls within the extension of that term or not. All objects in the extension of a given term have some common properties or characteristics which lead us to use the same term to denote them... The collection of properties shared by all and only those objects in a term's extension is called the intension or connotation of that term... Thus, the intension or connotation of the term "skyscraper" consists of the properties common and peculiar to all buildings over a certain height; while the extension or denotation of that term consists of the Empire State Building, the Chrysler Building, the Wrigley Tower, and so on.

(Copi 1972: 112)³

3. More recently Copi has criticised this view and switched to the new essentialist theories of extension advocated by Putnam and Kripke (see Copi 1977).

However, although the simple description theory has been of great importance both in systematics and in philosophy there are three important criticisms which can be launched against the model as a naturalistic account of all classification procedures. These may now be considered.

The first criticism is that objects may deviate from the requirements of an identifying description without an accompanying change in a classification system being made. Consider what happened to the natural kind term "mammal" when the duck-billed platypus was discovered. Hitherto all mammals had been thought to bear live young in contrast to reptiles which layed eggs. The duck-billed platypus was egg-laying and if simple description theory is applied ought to have been regarded as belonging to the set "not-mammal". However, monotremes (of which the duck-billed platypus is an example) have hair and nipples and eventually came to be regarded as mammals. It could be argued that this simply changed the intension of the term "mammal", but further problems arise if this view is taken. For example, some fossil reptiles certainly had hair and may have had nipple-glands. Just what are the essential properties of a natural kind and how can we guarantee in advance that they will never be subject to revision? Apparently we cannot guarantee anything of the sort.

The second problem that can be raised against the simple description model is that objects can be found (or imagined) which fit every last requirement of an identifying description but which have further properties which make their classification problematic. Putnam(1975) gives some interesting examples. Thus, supposing half the pencils in the world turn out to be organisms?⁴ It is to be imagined that these "pencil-organisms" have all the superficial characteristics of pencil-artefacts, perhaps as a form of camouflage. Only electron microscope studies reveal the tiny nerves and other organs which show these entities to be biological in their nature. For these animal pencils

4. The example comes originally from the work of Rogers Albritton.

the identifying description has not changed but would scientists consider "pencil organisms" and "pencil artefacts" to be members of the same class? Surely not says Putnam and he concludes that:

It follows that 'pencil' is not synonymous with any description - not even with a loose description. When we use the word 'pencil', we intend to refer to whatever has the same nature as the normal examples of the local pencils in the actual world.

(Putnam 1975: 243, underlinings in original)

A more realistic example of a similar phenomenon occurs in fungal taxonomy. Fungi undergo radical changes of structure during the course of their life-style. In several instances, parts of the life-cycle conform to the identifying descriptions of other classes of organisms. Indeed for this reason these parts of the life-cycle have sometimes received taxonomic recognition as, for example, protozoa. And yet when these "protozoa" were observed changing into fungi they were quickly re-classified as fungi. Why was this? They still fulfilled the identifying requirements of protozoa?⁵

Thirdly, it can be argued that the simple description model, even if it overcame the two objections raised above, is inadequate as a solution to the problem of how classification is achieved. The problem of classification is that of how we are able to recognise one class of objects as distinct from another and by what criteria we are able to decide how best to sort out and designate different objects into different classes. Simple description theory solves both problems by postulating essential properties of identity which reside in the form (and occasionally in the function) of all members of a natural kind. However, as we saw in the last chapter the notion of what constitutes a 'property or character of a natural kind is itself problematical. And this is without even beginning to consider the problems raised above of how to sort out "essential" properties from "accidental" ones.

5. For some examples see Alexopoulos (1952). A similar episode in zoological taxonomy is discussed by Winsor (1969). Thus, barnacle larvae used to be classified as crustacea. It was only much later that these "adult crustacea" were observed changing into barnacles, a group previously considered to be molluscs. This discovery prompted a fresh inquiry into the morphology of adult barnacles and eventually both adult and larval forms were moved into the crustacea.

For these reasons philosophers have tried to formulate new theories of classification. It is to these alternatives that we can now turn.

Cluster Description Theory

Simple description theory asserts that a natural kind terms extension is determined by a conjunction of properties which governs that term's proper usage. These essential properties make up the intension of the natural kind term and intension determines extension.

One way of overcoming some of the problems associated with this view of classification while retaining most of the elements of the traditional view of meaning (i.e. that intension → extension) is to conceive of the intension as consisting not of a conjunction of properties but of a cluster of properties. Thus, for a proponent of this view, no single property of a natural kind is essential to its classification but a sufficient number from the cluster of characters or properties is required.

This theory of classification is best illustrated by example. Consider the following four 'objects':

ABCD

BCDE

CDEF

EFGH

On simple description theory if the letters A, B, C etc. stood for essential properties then there is no way these 4 entities could be placed into a single class. However, for a cluster description theorist they might be so classified. If the eight properties ABC ... H are all regarded as important but not necessary properties and if possession of four or more of these properties is regarded as both necessary and sufficient for class membership then we are back to a position where:

I —————→ E
(Cluster of Identifying
descriptions)

Only now the intension is a cluster of properties instead of a conjunction. In the language of modern systematics a class of this kind would be polythetic (see Chapter 1).

Searle argues that a cluster description theory of this kind is applicable to our usage of proper names.⁶ However, as Searle also makes clear, the notion of "sufficient number of properties" is rarely laid down in advance:

Suppose we ask users of the name "Aristotle" to state what they regard as certain essential and established facts about him. Their answers would be a set of uniquely referring descriptive statements. Now what I am arguing is that the descriptive force of "This is Aristotle" is to assert that a sufficient but so far unspecified number of these statements are true of this object. Therefore, referring uses of "Aristotle" pre-suppose the truth of certain uniquely descriptive statements, but it is not ordinarily to assert these statements or even indicate which exactly are presupposed ... The question of what constitutes the criteria for "Aristotle" is generally left open, indeed it seldom in fact arises, and when it does arise it is we, the users of the name, who decide more or less arbitrarily what these criteria shall be. If, for example, of the characteristics agreed to be true of Aristotle, half should be discovered to be true of one man and half true of another, which would we say was Aristotle? Neither? The question is not decided for us in advance.

(Searle 1958: 171)

One immediate point which philosophers might take as an objection to Searle's analysis is that it makes classification a matter of choice rather than logical necessity. As a matter of fact cluster description theory of the Searlian kind could easily be developed to overcome this objection. If the properties of a class were laid down in advance and if the notion of what constituted a "sufficient number" of such properties was made explicit as well, then there would be no choice in deciding whether or not Aristotle really existed (provided that is, that everybody agreed to stick by the rules of the classification and everybody agreed what Aristotle's identifying description was composed of). A classification model of this type could perhaps be described as a "logicalised cluster description theory". However, from a naturalistic perspective such a development would be counter-productive. Searle is surely right when he claims that the properties

6. In taking Searle's account as being applicable to natural kind terms as well we are following conventional and accepted philosophical practice (cf. Schwartz 1977; and also Putnam 1975: 152).

of an identifying description are rarely set down in advance and that the concept of sufficient number of properties in a cluster is rarely made explicit. They could be set down in advance and in certain procedures in modern taxonomy they are explicitly verbalised (see the discussion in Appendix A of Numerical Taxonomy). However, this is not the usual way that taxonomists proceed to construct a classification and even here choice is not really eliminated since what counts as a character or property has still to be decided and so does the number of those characters which will be sufficient for membership of the class. Such a procedure does not eliminate subjectively from classification; it simply removes it to a stage before the actual making of the classification itself.

The advantage of cluster description theory is that it removes the problematical distinction between "essential" and "accidental" attributes or characters. On one reading of cluster description theories, at any rate, all the properties of a natural kind are potentially usable in that natural kinds classification.⁷ And if this position is taken then we have the kind of classification procedure advocated by phenetic taxonomists. Possession of no single property or even conjunction of properties settles matters in advance. All characters must be considered and weighed equally.

However, as both Putnam (1975) and Kripke (1972) have pointed out, description theory, even in this "cluster" form, inherits most of the problems inherent in simple description theories. What is common to both versions of description theory is their claim that a set of identifying descriptions (the Intension) determines the extension. Entities such as organismic-pencils, robot-cats and silicate-lemons remain just as problematic for this position as they did before. In all of these cases the entities imagined conform to the terms identifying description but would (arguably at least) not be considered to lie within the extension of the natural kinds pencil, cat and lemon respectively.

7. Although it must be remembered here that properties or characters are themselves human constructions. The number of properties or characters in, say, a buttercup is infinite so that the idea that "all" properties can be used in a classification is something of a fiction.

As Putnam puts it, "the sense in which literally anything with the superficial characteristics of a lemon is necessarily a lemon, far from being the dominant one is extremely deviant. In that sense something would be a lemon, even if it had a silicon-based chemistry, for example, or if an electron-microscope revealed it to be a machine" (Putnam 1975: 239, underlinings in original).

The discovery that identifying descriptions, even of a cluster type, do not provide a basis for determining the extension of a natural kind term suggests two possibilities. One is that the notion of extension should be retained and that we should seek elsewhere for an explanation of how extensions are determined. This is the path taken by Putnam and the new essentialist school of classification theorists. The second (and more radical) move would be to abandon the idea that extension is pre-determined by anything. Both of these possibilities will be considered in later sections, but we will begin with the first possibility, i.e. that extension is determined, but not by identifying descriptions.

Putnam and the New Essentialist School of Classification Theory

As we have just demonstrated above, traditional accounts of classification, both of the conjunction and cluster types, are linked with a theory of meaning which divides meaning itself into two components; intension and extension, and postulates a relationship of the form:

$$I \longrightarrow E .$$

Now, a problem which has concerned philosophers for a long time is the question of what metaphysical status to ascribe to intensional properties. According to Putnam, intensional meanings were traditionally conceived as being in some manner mental entities and were thus thought to be private to the individual observer. Frege, and later Carnap, objected to this 'psychologistic' interpretation. For Frege intensions are public properties and their existence is real and independent of psychological awareness. Indeed, this explains why for Frege and Carnap intensions can be 'grasped' by more than one person and by different persons at different times (Putnam 1975: 134).

However, as Putnam points out, this apparently radical move from a subjective to an objective account of intension is in fact not nearly

as far-reaching in its consequences as first appears. For even if intensional properties are conceived of in this manner, "grasping" the nature of such properties must still be a psychological act. And we are still working here within the framework of a traditional account of meaning. All that has taken place is a move from a relatively simple model of the form:

$$I \longrightarrow E$$

where I is the intension or essence of a term conceived of as a mental substance, to a slightly more complex model of the form:

$$P \longrightarrow I \longrightarrow E$$

where P is a (presumably learned) psychological state or condition of memory etc. and I the terms intensional component of meaning now conceived of as a public entity with an objective existence. Either way, extension in the last analysis becomes dependent upon a psychological property and this Putnam will not accept:

We claim that it is possible for two speakers to be in exactly the same psychological state, ... even though the extension of the term A in the idiolect of one is different from the extension of the term A in the idiolect of the other. Extension is not determined by psychological state.

(Putnam 1975: 139).

Putnam sets out to prove this assertion with the aid of three examples referred to below as the "Earth/Twin Earth Water example", the "Aluminium-Molybdenum example" and the "Elm-Beech example" respectively. Let us briefly examine each of these in turn.

1. The Earth/Twin Earth Water example

Imagine there exists, somewhere in the universe, a planet which is identical to Earth in all but one respect, namely that on this planet "water" has the same macroscopic properties as water on Earth but a different microstructure. Let us call this chemical structure, which is quite different from H_2O , XYZ.

Earthians, say Putnam, on reaching Twin-Earth in their spaceships, may at first confuse Twin-Earth water with the real thing. However, upon discovery of their mistake they will report back to Earth something like: "On Twin-Earth the word 'Water' means XYZ!" They will not report back: "On Twin-Earth water is XYZ!" And we would wish to say

here that the term "water" has different meanings on the two planets. On Twin-Earth water, what we call water, simply does not exist. And vice-versa. The extension of "water" in the Earthian sense (water E) is the set of all molecules of H_2O (or something like that); similarly the extension of "water" in the Twin-Earthian sense is the set of all molecules of XYZ.

But now imagine the state of affairs on Earth and Twin-Earth in 1750, before scientists on either planet had discovered the micro-structural properties of their respective water. Here Earthians and Twin-Earthians would apply the term "water" to different extensions or sets even though the intensional properties would have been identical and they would be in the same "psychological state". It follows that here is one case at least where the move $P \rightarrow I \rightarrow E$ appears invalid.

2. The Aluminium-Molybdenum example

Imagine a situation like the last one, but now on Twin-Earth what Earthians call Aluminium is called Molybdenum and vice-versa. Thus on Twin-Earth pots and pans will be made of molybdenum (in the Earthian sense) while on Earth they are made of Aluminium. Here again when space-ship travel gets going Earthian and Twin-Earthian speakers may be mistaken into thinking that the terms "Aluminium" and "Molybdenum" have the same extension on both worlds, and their psychological states when they utter the words "Aluminium" and "Molybdenum" will be identical. However, the first spaceman who is a metallurgical sophisticate will realise the mistake and discover that on Twin-Earth "Aluminium" is really Molybdenum and "Molybdenum" is really Aluminium. Here again we have a case where the psychological state of a speaker and the descriptive properties which he associates with a given term do not appear to determine the extension of that term.

3. The Elm-Beech Example

Putnam, as a botanical non-sophisticate, claims that his own mental concept of an elm tree and a beech tree are the same and he associates the same descriptive associations with each word. And yet here again we can say that the extension of "elm" and "beech" are, for Putnam as for anybody else, unchanged, viz. the set of all elm

trees and all beech trees respectively. Here again a move of the form $P \rightarrow I \rightarrow E$ is invalidated.

These then are Putnam's arguments for rejecting traditional accounts of meaning and reference. Other philosophers have recently put forward equally cogent arguments for taking the same view.⁸

What else can be learnt from these examples? The last two examples demonstrate what Putnam calls a division of linguistic labour. Thus anyone who uses terms like "elm" and "beech" or "Aluminium" and "Molybdenum" does not, of necessity, have to acquire the means of recognising the members of the extensions which these terms denote. How many city financiers who deal in gold stocks can tell the difference between gold and all other metals? The reason for this is that other members of the community (the experts) can determine the reference of these terms. And Putnam, plausibly enough, argues that this division of linguistic labour is in turn based upon the division of labour within society.

However, Putnam also uses the examples discussed above to make a far more contentious point. This is the claim that natural kind terms are indexical expressions and that they act (in Kripke's terminology) as rigid designators (Kripke 1972).

The force of this argument is best illustrated by example. Consider again the Earthian and Twin-Earthian usages of the natural kind term "water". As Putnam says there are two theoretical glosses which can be used to interpret what is happening here:

1. That "water" is a world-relative term. By this theory "water" means water on both worlds but it just so happens that water on Twin-Earth (W_2) has a different molecular structure from water on Earth (W_1).
2. That "water" on W_1 and W_2 means different things. By this theory water is always H_2O and it follows that the stuff called water on W_2 is not, ipso facto, water.

For Putnam there is no question that of these two approaches theory (2) is the one which is correct. What implications follow from this?

8. Most notably Donnellan (1966). As Donnellan shows it is possible for reference to take place not only in the absence of an identifying description but even where that description is false.

Basically it follows that ostensive definition provides a rigid designation for the extension of natural kind terms. When I point to a beaker of liquid on Twin-Earth and say that it is water, what I mean is that it bears a same-essence relationship to water on this world, Earth.⁹ If this same_e relationship does not in fact hold, then I am mistaken.

Once we have discovered the nature of water nothing counts as a possible world in which water doesn't have that nature. Once we have discovered that water (in the actual world) is H₂O, nothing counts as a possible world in which water isn't H₂O. In particular, if a 'logically possible' statement is one that holds in some 'logically possible world', it isn't logically possible that water isn't H₂O.

(Putnam 1975: 150-151, underlings in original)

A natural kind term may be in usage for a long time before a cross-world relation of this kind is established. But, when such a relationship is discovered, it means that the extension of the natural kind term is fixed for all possible worlds. The argument is not that the existence of such a relationship is an epistemic necessity. We may never know with absolute certainty whether our classifications do reflect the essential properties of natural kinds (although in science especially it is intended that they should do so). Rather the argument is that the existence of such cross-world relationships is a matter of metaphysical necessity. And to take such a position one has to be a realist not just in the sense of believing that a real world exists, but in the much stronger sense of believing that it is the nature of that real world which determines the correct usage of natural kind terms.

Again, to clear up another point of possible misunderstanding, Putnam is not arguing that natural kind terms in current usage in our language must of necessity apply to substances with a unique physical basis. It could have turned out that water had two or more molecular structures. But in this case it would really be two natural kinds and not one. An interesting example of this which Putnam discusses is Jade. Although all jade has the same superficial characteristics it is in fact composed of two minerals, jadeite and nephrite, which are chemically quite distinct.

9. What Putnam means by the concept of a 'same-essence' relationship will be considered in the next section of this chapter.

Indeed, Putnam even concedes that there may be some natural kind terms which apply to substances or objects with no shared micro-structural properties at all. But in this case the terms extension will be fixed in a way which is quite different.¹⁰ Also, natural kind terms of this sort will be common in lay language but increasingly rare in science. For it is the task of science precisely to discover the true essences which underlie the superficial appearance of the natural world.

In its positive aspects then, Putnam's work amounts to nothing less than a new theory both as to the nature of meaning and the nature of reference. Let us consider meaning first. Meaning is traditionally divided into two components: intension and extension. Putnam keeps the notion of extension more or less as before, but he denies that intension determines extension. Instead extension is determined by the discovery of cross-world relations or essences and science is conceived of as an enterprise whose function is the discovery of these essences.

This, then, is the first radical and new departure in Putnam's theorising about meaning. The second novel feature in Putnam's account, and it is a feature which we have not dealt with hitherto, is Putnam's introduction of the notion of stereotype. To understand the necessity for this notion we may consider again Putnam's deplorable, but understandable, ignorance concerning the difference between elm trees and beech trees ("the elm-beech example"). Putnam knows that the terms "elm" and "beech" denote different physical objects and that the terms have, therefore, different extensions. However, a botanical sophisticate might well still want to argue that Putnam does not understand, or at any rate does not fully understand, the meaning of the terms "elm" and "beech". Why is this? It is because Putnam does not know the properties of elm and beech trees which would allow him to correctly assign examples of each tree to their correct class (e.g. that beech trees have fruits and leaves of a certain type; that elm trees have fruits and leaves of another quite different type etc.). Descriptive properties of this sort, which typify a natural kind, form the stereotype of that term. Stereotypes are important in language, and communication without them would be impossible. But, and this is the central point, stereotypes

10. In fact via a cluster of descriptions in the manner discussed by Searle (see Putnam 1975: 159).

do not determine extension.¹¹ That role, as we have seen, is allotted to cross-world relationships or essences.

Stereotypes and cross-world relations solve some of the philosophical problems concerning meaning, but problems still remain when we come to consider the notion of reference. The traditional theory of reference centres on the old idea of intension (see Schwartz 1977: 13). A general term or name refers to whatever fits the characteristics the term or name means. However Putnam denies that names have an intension in this sense. In place of the descriptive theory of reference Putnam, and others, have argued that reference is established by something like a causal chain (see especially Putnam 1973). When a name is first connected to a referent this involves a kind of "baptism". As long as later speakers in the chain intend to use the reference in the same way, successful acts of reference can be accomplished. When we refer to a term it is, therefore, not necessary to know the nature of the stuff we are naming. I may know nothing about electricity except that its presence in some mysterious way is connected with what does or does not happen when I switch on a light bulb. However, I can still make statements which are acts of successful reference and which contain the term "electricity" because there is a ^{us}causal chain leading back from my use of the term to its original usage in the science of physics.

How does all this shape up as a naturalistic theory of classification? Putnam clearly intends that his work should be taken in this way, for in the introductory remarks to his paper on The Meaning of Meaning he states the desire that his work will prove to be of value to linguists and other social scientists interested in the problems of language and syntax. However, as will be demonstrated in the next section, Putnam's work does not provide the basis for the naturalistic theory of classification for which we have been searching.

Putnam's Theory of Classification: a critique

The criticism of Putnam's work which follows can be stated in its bare outlines by means of the following five propositions:

11. Stereotypes are thus very like intensions or identifying descriptions but differ because they do not determine the extension of a natural kind term.

1. That Putnam's theory of classification is one which is essentialist.
2. That scientists themselves are often explicitly anti-essentialist in their self-conceptions of how they practice classification.
3. That scientists are frequently anti-essentialist in their practice.
4. That Putnam is in no position to judge this to be unusual or deviant practice on the part of these scientists.
5. That the actual essentialism Putnam holds to describe scientific classification is itself obscure since he does not adequately analyze the nature of what is involved in a "same-essence" relationship.¹²

That Putnam is an essentialist is not, we would suspect, a charge which he himself would wish to deny. Popper in an often quoted passage from The Open Society and its Enemies defines essentialism as, "the view, held by Plato and many of his followers, that it is the task of pure knowledge or 'science' to discover and describe the true nature of things, i.e. their hidden reality or essence." (Popper 1950: 31). As we have seen, Putnam holds precisely this position and it is to science to which he looks for the discovery of these 'cross-world relationships' or essences.

Essentialism seems an odd label to attach to Putnam's work because, as a matter of historical contingency, essentialism in the past is a philosophy which has often been associated with idealist metaphysics. Putnam garbs his essentialism in the cloak of a realist metaphysics, but his doctrines remain no more-or-less essentialist for all that this is the case.

Now the first point which can be made about Putnam's claim that science uncovers hidden essences which then provide the basis for

12. These criticisms will be mainly directed at Putnam's analysis of meaning. The causal theory of reference which Putnam presents can also be challenged from a naturalistic position. Thus, Kleiner (1977) has shown that a casual theory of reference does not (contra Putnam) entail that referential divergence may not occur during the history of a sciences development. A casual theory of reference is illuminating, but only if it is viewed as describing a network of beliefs which are socially transmitted (Kleiner 1977: 108).

classification is that if Putnam is right then scientists themselves have become curiously deluded about the real objectives of their research. For, as we saw in Chapter one, professional taxonomists are openly hostile to philosophical essentialism, and have deplored the "typological thinking" which results when such philosophical canons are pursued. Indeed one distinguished scientist and historian of taxonomy has gone so far as to argue that the removal of essentialist thinking from taxonomy has been the major factor in the progress which has been made in taxonomy during the period since Darwin:

The assumptions of population thinking are diametrically opposed to those of the typologist. The populationist stresses the uniqueness of everything in the organic world. What is true for the human species - that no two individuals are alike - is equally true for all other species of animals and plants... All organisms and organic phenomena are composed of unique features and can be described collectively only in statistical terms... For the typologist the type (eidos) is real and variation an illusion, while for the populationist the type (average) is an abstraction and only the variation is real. No two ways of looking at nature could be more different.

(Mayr 1976: 27-28)

Thus, when a modern taxonomist points, for example, at two herbarium specimens and makes an assertion of the form that, "these herbarium samples X and Y both belong to the same species Z", he is generally not postulating a same-essence relationship between them in the sense (if there is a sense) in which Putnam uses this term. There was a period when it was thought that the classification of species was possible using this kind of approach. But today even herbarium taxonomists, who in the past were the firmest adherents to this view, are firmly committed to populationist principles, which deny the search for essential properties in species, and which stress the uniqueness of everything in the organic world.

Does this mean that we can dismiss Putnam's work already as a naturalistic solution ~~to~~ to the problem of classification? It may seem strange that Putnam knows the true nature of taxonomy better than taxonomists themselves seem to know it, but in fact this is far from conclusive. Scientists, like the rest of us, are not infallible. It could be argued that given more time and new techniques, the present pessimism within the biological community concerning their ability to discover the essential properties of natural kinds might

conceivably be changed. So we must give Putnam the benefit of the doubt on this occasion and seek more compelling reasons for doubting the views on classification which he sets forth.

Much more compelling is the fact that the actual practice of scientists when producing classifications is often carried out in a manner which is contrary to Putnam's predictions. Other examples will be considered in the historical material which follows, but for the moment we can reconsider the practices of numerical taxonomists described briefly in Chapter one. As was explained in Chapter one the principle behind numerical taxonomy is that of equal-weighting of all characters used in the construction of a classification. As wide a selection as possible of characters are coded in mathematical form, and the computer is then used to ensure that all of these characters are treated as having equal value with no a-priori weighting. The resulting classifications are phenetic, i.e. based solely upon overall resemblance or similarity, rather than phylogenetic, a point which numerical taxonomists argue is of great value because it removes the kinds of phylogenetic speculations and assumptions (both explicit and implicit) in other forms of taxonomic procedure.

Within numerical taxonomy no character is treated as more important than any other let alone as essential. All characters whether morphological, anatomical or biochemical are given equal rank. And yet numerical taxonomy is a part, and indeed a significant part, of current taxonomic science. Of course, Putnam is at liberty to argue that numerical taxonomy is bad science but, from a naturalistic perspective, we may simply note that it certainly is accepted as a part of taxonomy. It exists, and a naturalistic theory of classification must take account of its existence. It is not of course, the case that all taxonomists denounce essentialism in this manner. For example, as is shown in Chapter five, many experimental taxonomists have maintained (and still do maintain) that the micro-structural characters of plants are more important in classification than "superficial" external characters. However, for Putnam's theory to hold it would have to be demonstrated that numerical taxonomists are acting illogically or irrationally in persisting to deny such claims and Putnam provides no grounds whatsoever for the warranting of such a conclusion.

In summary then, the beliefs and practices of working taxonomists call into question the validity of Putnam's theory. But even in its own terms there are inconsistencies and ambiguities of presentation which raise serious problems in Putnam's account. Putnam asserts that same-essence relations determine the extension of a term. However, same-essence relations do not exist until they are chosen as part of the development of a classification strategy. Before this step is taken any number of similarity relations exist which might be considered as essential.

Thus, even within essentialism options remain. An interesting case discussed by Mellor (1977) concerns the discovery of isotopes of chlorine. Here if electronic microstructure is regarded as the essence of chlorine then the two isotopes are the same kind. But, if nuclear microstructure had been regarded as the essence of chlorine then two natural kinds would have been "discovered". In fact we took the first of these options, but both were possibilities. And, this being the case, the extension of the term chlorine could not have been fixed in advance on this world, let alone all possible worlds.

If what has been said so far about "the new essentialism" is correct then it would be legitimate to enquire as to why talk of essences, cross-world relations, rigid designation and the like has proved so seductive to philosophers of science like Putnam. What makes the theory appear so attractive? As Mellor (1977) has pointed out in a valuable criticism of the writings of Putnam and Kripke, much of the apparent force of the argument stems from the exemplars chosen to present it. For example, in the elaboration of his idea Putnam pays particular attention to the use of chemical natural kind terms; water is a molecule of a certain kind, gold is an element with a certain atomic number etc. These examples have force because they are particular essentialist strategies which carry the authority of science. And yet even in cases like these only a little imagination is needed to see the fallacy of the position which is taken. Imagine the hypothetical, but plausible, case of a society which like ours, uses gold in its economy as money, but which means by "gold" not only what we call gold, but all other metals which bear golds superficial characteristics. Imagine in addition, that this society has no

institution within it comparable to modern chemistry. On learning from an outside source (or even from a typical insider whose hobby happens to be chemistry) that their gold is "really" more than one natural kind because different exemplars of gold have different atomic numbers and the like, what is the likely response? Is the society likely to change its system of classification with respect to the natural kind term Gold? Surely not. The claims of the outsider, if they are believed at all, are surely more likely to be dealt with as a manifestation of the existence of different microstructural properties in a single natural kind than as the discovery of a hidden essence revealing a previous error in the classification.

It is not, of course, the argument here that events would have to go in this way. But the events could proceed as described above and if they were to do so there would be no grounds whatsoever for saying that the community acted in a manner which was illogical, irrational, or against nature. Treating "gold" as one or many natural kinds here would be two equally feasible options available to the culture. A change in the classification might aid some parts of the culture (amateur chemists, for example) but others might find life more difficult (buyers and sellers would no longer be able to tell gold from non-gold on sight). The likely forecast here is that there would be no change of classification because this option preserves forms of social life around existing categories and values. But the fact that there is choice at all suggests that extension is not determined in all possible worlds by the discovery of same-essence relationships. Rather different classificatory strategies are possible without semantic deviance and these will differ from culture to culture.

Putnam himself sometimes comes close to admitting that there is a goal-related choice available in the way people develop classifications. Thus we are told at one point (Putnam 1975: 157) that substances share the same-essence when they agree in important physical properties but that "importance is an interest-relative notion". However, at other points in his account this insight appears to be lost. Thus, in the conclusion to the same section of his essay Putnam (1975: 160) argues that the " H_2O -ness" of water determines what we can and cannot counterfactually suppose about the natural kind water.

If the definition of water as that which is H_2O is a choice how can this be?

This inconsistency emerges even more clearly in an earlier discussion of indexicality and rigidity. There Putnam (1975: 151) says that, "it is conceivable that water isn't H_2O ... but it isn't logically possible!" But if it is conceivable that water isn't H_2O then just what kind of "logic" is being invoked here? Is Putnam saying that although other cultures may not classify substances by microstructural properties they will be acting illogically in making such a choice? If so, he gives no grounds for substantiating such a claim.

In order to drive home this last point and to summarize the general arguments presented in this section of the chapter, we shall consider one more hypothetical exemplar. This time, however, we shall move a little nearer home by considering, not a chemical natural kind, but a biological one. Imagine then that contrary to all expectations, the next Mariner probe on Mars discovers the hitherto unknown existence on that planet of a race of Martian tigers. We shall suppose that these tigers have the same superficial characters as tigers on Earth, and the same internal structure as well. Thus, on their return to Earth cytological and genetical analysis will reveal cellular details and a genetic code (D.N.A.) identical in type to those of tigers on Earth. Also let it be the case that breeding tests between Earthian and Martian tigers prove successful, so that crosses between the two groups produce fertile offspring identical in form and variation with their parents. However, let us finally suppose that the situation pertains whereby there is very good evidence (e.g. in the fossil record on Mars) for the hypothesis that Earthian and Martian tigers have a completely different ancestry and that they evolved in total isolation from one another. What is happening here, apart from a truly remarkable case of parallel evolution? How many natural kinds are we dealing within this instance : one or two?

It is difficult to state in advance how professional taxonomists back on Earth would deal with a case of this nature. However, to judge from writings in contemporary systematics there would be considerable

controversy on the issue. Phenetic taxonomists (which as we saw in Chapter one would include numerical taxonomists and some orthodox taxonomists) would presumably class Martian tigers and their Earthian counterparts into the same taxa, for in terms of a classification based on overall resemblance there would seem to be no good reason not to take this step. Strong adherents of a "biological" species concept would also, though for different reasons, approach the problem in this manner as well because they would point to the fact that Earthian and Martian tigers were capable (potentially at least) of gene-exchange. And if Putnam is correct we must, as a matter of logical necessity, talk in terms of only one natural kind being apparent, because the same hidden (and for that matter superficial) structure has been postulated to exist in both groups. Yet many (and indeed probably the majority) of modern taxonomists would resist this view. Most taxonomists would be likely to argue that biological classification should reflect phylogenetic relationship and, as we have already postulated, there is good evidence in this instance that Martian and Earthian tigers have arisen from completely independent phyletic lines.

Again, it is not the argument here that events would necessarily have to develop in this way. In trying to judge what would happen on the basis of current debates within plant systematics we are making guesses about events where relevant causes do not yet exist. But suppose a controversy of the kind we have just envisaged did take place. In what sense would one side be right and one side wrong? Would an assymetric approach to understanding what had taken place be justified? Are phylogeneticists all holders of a theory of gospel truth and pheneticists deluded fools? Or vice-versa? If philosophers think that they can genuinely answer these questions then they are in the wrong profession. They ought to be taxonomists.

This last example suggests that people invent and decide their classification in ways which are not layed down in advance. Moreover, there would appear to be no context-independent method of deciding in this case which classification of Martian tigers is the "correct" one. A naturalistic theory of classification must take these facts into account and for this reason the new essentialism must be rejected as a starting point for our purposes. What is required is an account

which recognises that future usage of terms is not pre-determined in advance. That future usage exists only when people have developed it. That options are available in that development, means that we have to ask why one option rather than another is collectively selected. Does such a starting point exist? Fortunately, the answer to that question is that it does. It can be developed from the recent work of another philosopher of science, Mary Hesse.

The Network Model of Classification

The work which Mary Hesse has done on classification is derived from concerns of a somewhat different nature from the objectives of the New Essentialist school of Kripke, Putnam et al. As we saw, the new essentialists have been concerned primarily with the philosophical problems surrounding the notions of meaning and reference. Mary Hesse's work also has profound implications for this area of philosophy, but its initial development stems from Hesse's earlier writings both on metaphor and on the search for an independent observation language in science (Hesse 1958, 1963). Hesse's major contribution to the philosophy of science has been conclusively to demonstrate that no such independent observation language exists. The usage of all predicates in a language is potentially revisable and the distinction between "observational" and "theoretical" terms in science is purely a relative one.

In what comes next we shall not be following in detail Hesse's elaboration of the network theory of classification (see Hesse 1974). Instead we shall develop those elements of her work of greatest utility to the formulation of a naturalistic perspective on this subject. The section which follows also relies heavily on an unpublished paper by Barry Barnes (1978).

The different starting point of Hesse's work can best be illustrated by a consideration of what is common to both descriptive and essentialist theories of classification. Proponents of both description theory and the new essentialism assume that natural kinds have surface or hidden features and they assert that it is these features which determine a correct classification. Arguments occur between proponents of the two positions over the nature of these

features (in one case they are intensional properties or identifying descriptions, in the other hidden essences or same-essence identities). However, that a terms extension, and hence its meaning, is determined in some manner is an assumption of both theories.

Let us for a moment set aside the question of how (if at all) extension is determined and consider two other problems which must be at the root of any naturalistic account of classification. Firstly, what is the nature of the information on which classifications are based? And secondly, how are classifications learned and transmitted?

Any answer to the first question must recognise that learning takes place through the assimilation of information from the environment. Of the ultimate metaphysical make-up of this information nothing need be said. What is clear, however, is that the environment is very rich in information. And, more specifically, every physical event and object is, in principle, unique. No two cats, for example, ever have exactly the same physical attributes, nor do they ever behave in exactly the same way. In all cases we can recognise both similarities and differences between any two objects or physical events. (The consequences of this for any naturalistic theory of classification are profound as will be demonstrated below.)

Having recognised the role of the environment, and the information it provides, we must also recognise that this is an insufficient basis for most forms of learning because learning normally requires a teacher. A cultures classifications of its environment are not learned (or produced) simply from a passive examination of that environment. They are learned in a three-way interaction involving both the world (or perceptual input), the learner and whoever is teaching the learner. Learning a language is a social process and cannot be carried out in the absence of social interaction. The question, as we shall see, is not whether learning a classification is a social process, but rather what kind of process (or processes) are involved?

Let us consider what processes and procedures are available to a teacher when he tries to impart his cultures classifications to a neophyte. Developing an example used in a recent paper by Kuhn (1974), imagine a child's first visit to the Zoo. While in the zoo, this

child is taught the meaning of the terms "swan" and "duck". How are these terms usages transmitted to the child? Basically, two learning processes are involved.

1. Ostension. The child is shown various examples of ducks and swans and told: "that is a swan!" or "that is a duck!"

2. Verbal description. The child may also be told certain general laws about swans and ducks to aid this identification. "Ducks are small birds which quack" and "swans are large white birds which honk" might be two such verbal descriptions which are given.

However, of the two learning processes which are involved here it is ostension which is the more fundamental. Learning by verbal description always involves new terms which have themselves to be understood. In the example above "largeness", "smallness", "white", "quack" and "honk" are all such terms. Perhaps some of these terms could be further described, e.g. "large birds are birds over one foot in length" but the neophyte must know what "one foot" and "length" are. There is an infinite regress, unless we accept that learning ultimately depends upon ostension and that ostension itself consists of pointing to instances of physical objects and events which are actually unique.

The network theory of classification, then, is predicted^a upon a theory of human perception which claims that our ability to classify depends upon our recognition in the environment of similarities and differences in objects. Also, it follows that these primary processes of recognition are, in the last analysis, unverbaised. If they were verbalisable then the act of verbalising them would require predicates which in turn would have to be learnt by ostension, so unless we introduce at some point a non-linguistic component to perception we are trapped in an infinite regress.

It is of some significance, therefore, that professional taxonomists whose day-to-day activities centre around classification hold to a similar position. According to such taxonomists, character recognition, on which species-making depends, relies upon unverbaised perception, at least in the first instance. It is only later, when

the taxonomist has "got to know" the group on which he is working and has a fair idea of the number of species involved and how he is going to separate them, that he "rationally reconstructs" his intuitions concerning the group and locates the characters which will serve as markers for his taxa. In writing a monograph on a new and little understood genus the keys are not written first, rather they are normally written last.

Generalising the position outlined above and putting it into a formal framework, we get a model of the sort illustrated in Figure 2.1. In this diagram C_1, C_2, C_3 etc. represent concepts or terms in general use within a culture. For convenience, these can best be thought of as natural kind terms, "fish", "whale", "mammal" and the like. I_1C_1, I_2C_2, I_3C_3 , etc. are particular instances or paradigm cases of such terms whose number is finite for any given culture. And finally in Figure 2.1. we have the law like connections which bind the system of classification into a coherent whole: all swans are white, all ducks are small water-fowl etc. The p here stands for a probability function, for not all law-like connections have a $p = 1.00$. Not all swans are white for example, although most are. Probabilities will rarely be stated explicitly, although of course they may be. It is also perhaps worth noting that p may be taken to be 1.00 even although the teacher of the law knows that it is not. The father may tell the child all swans are white even although he knows that some swans are black. As an ethnomethodologist like Garfinkel might say, swans are white for all practical purposes.

Seen in this manner then, the network is a model of the verbal component of our culture. It provides a pictorial representation of how we both classify the natural kinds of entities which exist in the world about us and account for the law-like generalities which hold between these natural kinds - between the classes of things which we ourselves have made. The knots of the net represent concepts "tied" as it were to reality by ostension. The linking strands of the net are the laws which bind together these concepts. To a first approximation the network may be regarded as stable for any given

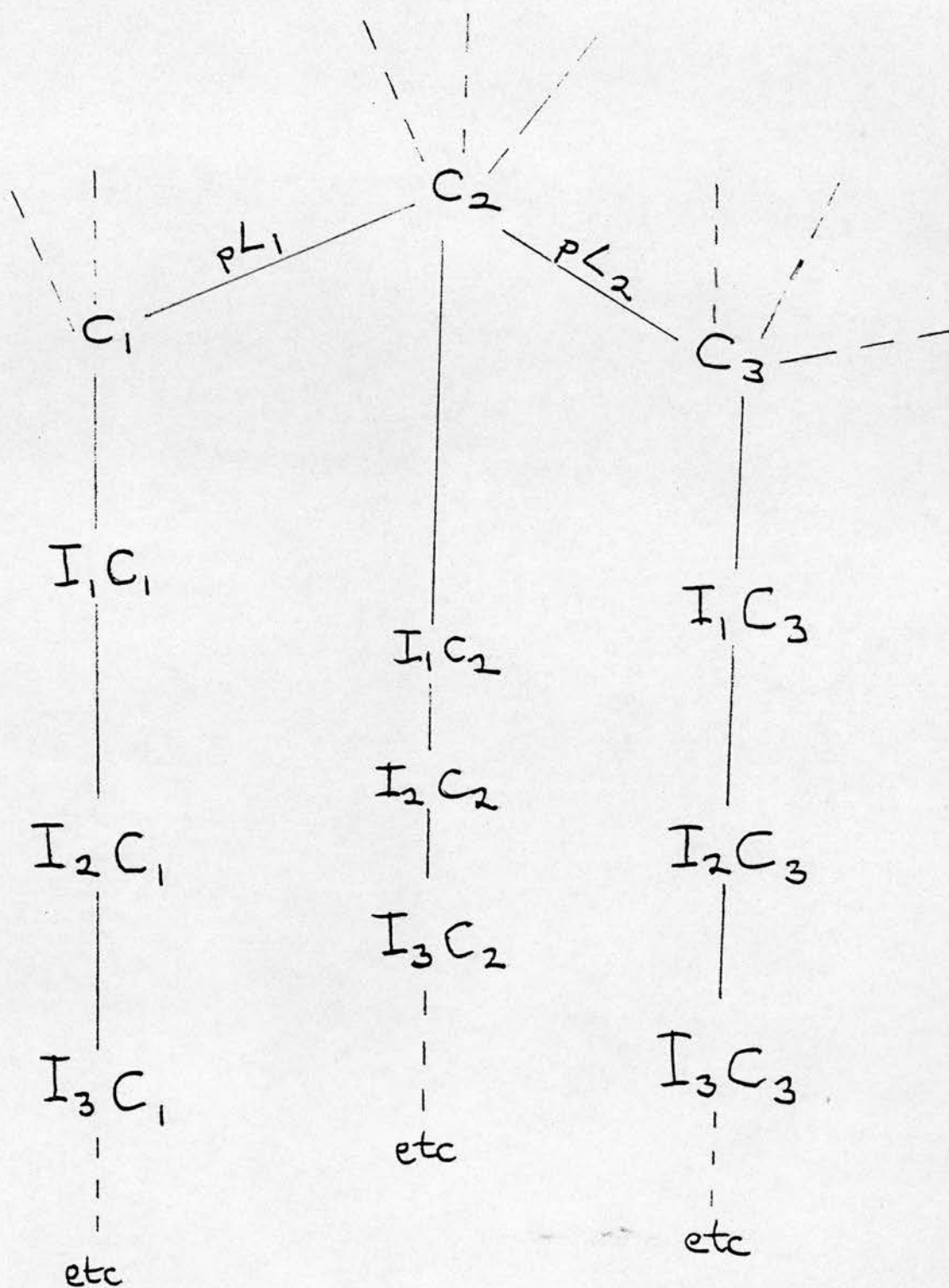


Figure 2.1. The Hesse Net (adapted from Barnes 1978). For explanation see text

culture. Note also that it is transmitted to neophytes through the usual culture channels - learning, demonstration, persuasion, threat etc. as deemed appropriate. In the first instance it is thus given for any individual within the culture.

A question of fundamental importance can now be addressed, namely, how does usage based on a network proceed? What determines which instances are subsumed under each concept or term in the net? As has already been indicated, similarity and difference relationships occur between all instances in the network. It follows from this that classification is always an act of judgement. Nothing guarantees that the next potential instance of a term may not prove problematical; no part of the net is of necessity never to be subjected to revision. Choice is always involved in the development of a classification. There is no natural or absolute basis for weighting similarities and differences. Actors choose to stress some similarity relationships over others or to play down some differences as compared to others. What dictates such choices? In the last analysis actors are always free to decide for themselves but what will clearly influence such choices are the goals or interests which the classification is designed to serve. Classifications are conventions designed to serve the objectives of those involved in the classifications construction.

The second contingency which will affect but not determine how a classification is developed is the pre-existing state of knowledge. New knowledge after its construction has to be "fitted into" what has gone before. That fact is something which the human being creating the new knowledge has to take into account. The growth of culture is, in the last analysis, an evolution not a revolution; otherwise communication would break down and we would talk of a new culture replacing an old one, not of an old one growing.

It is now possible to see that both descriptionist and essentialist theories of classification fail as naturalistic theories because they do not take account of the conventional nature of classification. Extension is not determined either by identifying descriptions or by the discovery of hidden essences, because stressing one or other of these factors is itself a choice. However, it remains true, as will

be shown in later chapters, that both description theory and essentialist theories do describe possible strategies for constructing classifications. And in the recent history of botanical systematics both strategies have been (and still are) deployed.

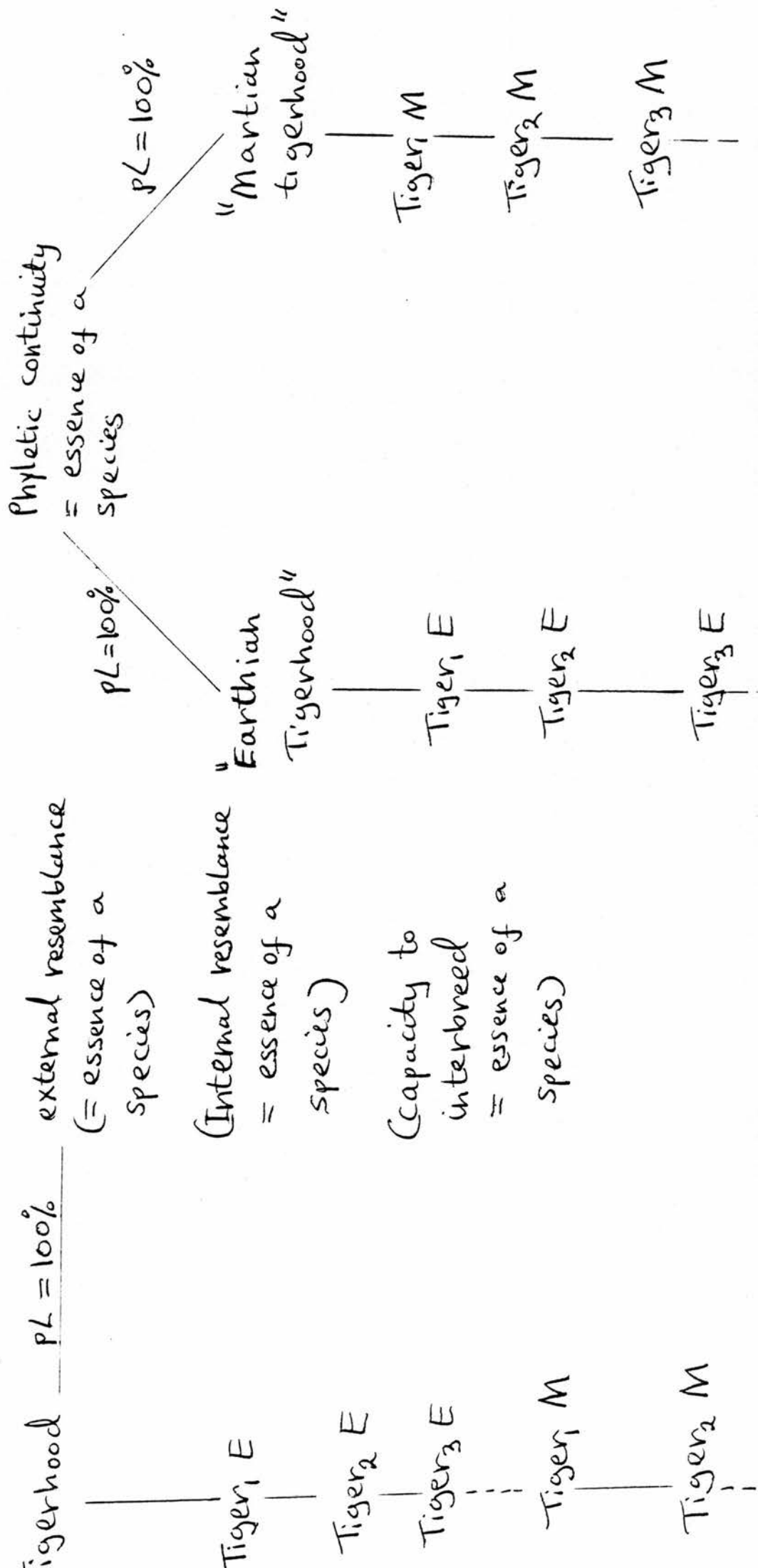
This last point can be further illustrated by reconsidering an example discussed earlier. Consider again the case of Tigers on Mars. No less than four "essential" properties of "tigerhood" could be postulated on the basis of this example (see Figure 2.2); all can be thought of as possible strategies for the development of the usage of a network of terms.

1. We could equate the concept of tiger with sufficient resemblance of an external appearance.
2. We could equate the concept of tiger with sufficient resemblance of hidden structure.
3. We could equate the concept of tiger with capacity to exchange genes.
4. We could equate the notion of tiger with a concept like that of evolutionary or phyletic continuity.

Any of these four strategies for concept application becomes "essential" if we collectively choose to make it so, i.e. if we consistently deny apparent counter-examples by appropriate judgements of similarity/difference weightings. But none of these approaches conflicts with what we have postulated that we know about Martian and Earthian tigers. Rather, all four strategies are equally compatible with the facts as they are known. Essences of a kind may be maintained in Hesse networks, but they are conventions like any other part of the net.

Although the account of classification produced above has been constructed with different objectives in mind from those of most philosophers there is actually little in the assumptions that have been made that should be unacceptable to most current philosophers

Figure 2.2. Four Essentialist Strategies for Dealing with the Problem of Martian Tigers (for explanation see text).



of science. That reality exists and that its nature is sufficiently complex to allow many human interests of different kinds to become developed in dealing with it from diverse angles, objectives, perspectives etc. are both fairly non-controversial claims.¹³ The plausibility of both assumptions derives from the very diversity of beliefs about reality of which we know human beings to be capable. It is the proposition that classifications are conventions which is likely to arouse strongest passions. Most philosophers consider themselves to be realists and not conventionalists, even though there is no good reason why this should be the case. What are their objections to the label of conventionalism when applied to knowledge? We can do no better than examine the reasons given by the philosopher who was the source of inspiration for much of this section of the essay, Mary Hesse.

Hesse describes herself as a realist philosopher, although she admits that the difference between the "conventionalists" and "realists" is often one of different modes of expression rather than of issues of substantive disagreement (Hesse 1974: 56-61). Her own objections to "conventional talk" as applied to language appear to rest on two foundations, one an argument over theory, one a moral objection.

The theoretical issue is really dealt with quite easily. Hesse denies that her account of classification is conventionalist because such a view, she maintains, does not take seriously the systematic character of laws. This is simply not the case. Conventions are not mere conventions. Classifications and the system of laws which are associated with them are systematic because the human beings who make those laws have sustained interests and motives for taking the options they do in fact take and developing the knowledge in the way in which it is developed. We cannot predict in advance what will happen in any one instance because human beings are far too inventive

13. Although it is worth noting that the existence of reality appears to be denied by some extreme proponents of sociological relativism. Interestingly such beliefs often appear to be linked to a radical disapproval of science (for example, see Roszak 1970).

and resourceful to make such guesswork plausible. However, this does not mean that systems of classification are entirely random ad hoc affairs either. There is a link between interests and the growth of systems of knowledge and belief, as we shall demonstrate in the following chapters.

The moral argument also appears to be invalid and is indeed based upon theoretical argument already discussed. Thus Hesse appears to argue in one remarkable passage of her book that if we talk of language acquisition and usage in conventionalist terms then the world of "newspeak" is just around the corner:

The differences between the models (i.e. of conventionalism and realism) are more verbal than substantial but the model using the notion of truth is less open to the currently dangerous misinterpretation of mistaking brainwashing for objectivity.

(Hesse 1974: 61)

But this is emphatically not the case. True the conventionalist account does take notice of the fact that people are continually developing language to manipulate it for their own ends. But it is people not language which does the manipulating. If "they" are trying to usurp our language then recognition of this fact may actually help to prevent the nightmare world of Orwell's 1984.

With Hesse's claim that the issues between conventionalists and realists are more verbal than substantive, we can have much sympathy. Reading this controversy in philosophy it is an impression easily gained. Also we would be the last to argue that verbal quibbling should be allowed to stand in the way of genuine understanding. But the commitment to a realist metaphysics must be firmly resisted if it leads to a failure to take proper account of the role which interests play in the growth of knowledge. And we do not have to look far to see an example where this is the case, for Putnam's work illustrates beautifully how a realist-orientated commitment in metaphysics can lead to precisely this error.

Indeed our own account of the role which interests play in the growth of systems of classification need further elaboration. How and what role do interests play? What different kinds of interests



are involved? These are questions to which we must return. But to do this a new line of attack is required, for in any given instance these are empirical questions. To answer them we must leave, for a while, the grand palace of philosophical theory and enter the more humble abode of historical, empirical research.

Chapter Three: Attempts to Introduce Experimental Methods
Into Taxonomy prior to 1920

Orthodox taxonomy is essentially Linnaean both in its aims and practice. Indeed the development and long survival of what may loosely and generically be termed Linnaean methods is in itself of great interest and importance. The philosophical presuppositions on which Linnaeus based his taxonomy were probably derived in part from an early training in Aristotelian scholasticism. Linnaeus was an essentialist in the Popperian sense of that term (Popper 1962: 31; Stafleu 1971: 25-31). Thus, for Linnaeus species were objective entities, existing in nature and separated from each other by sometimes hidden, but nonetheless real, essences or characters. The taxonomist's purpose was to uncover these real essences or characters, and so to express the hidden order of the natural world. The most serious consequence of adopting such a position was that variation within the species played a very minor role in Linnaean taxonomy. It is true that the Linnaean system does possess a single category, the variety, which is below the level of the species, but, for Linnaeus, intraspecific variation was a comparatively unimportant matter, a result of cultivation or accident rather than of nature, and he never altered his view that varieties were epiphenomena unworthy of the serious botanist's attention (Stafleu 1971: 90-91).

However, in addition to conforming to these philosophical doctrines the Linnaean system was also designed to be eminently practical in its application. Apart from an early period in his life, Linnaeus travelled little and his observations of plants relied heavily on herbarium material (Stafleu 1971: 112-114). The Linnaean system, with its ordered hierarchy of class, order, genus, species and variety, allowed a systematic categorisation of plant species based upon a visual examination of the plant's gross external morphology such as is possible to perform easily on the dead plant material of the herbarium. In his reliance upon the external properties of organisms for constructing a classification Linnaeus was typical of naturalists of the classical period (cf. Foucault 1970); and in fact this reliance on external features for taxonomy shows not only in his writings on animals and plants but to a large extent in his writings on mineral

classification as well (Albury and Oldroyd 1977: 191-194).

The Linnaean method was designed to allow rapid and easy identification and naming of new plant material. Indeed, Linnaeus himself defined botany as, "that part of the natural sciences by which one obtains happily and easily a knowledge of plants and by which one uses that knowledge" (quoted in Stafleu 1971: 33). Emphasis on the practical, instrumental aspects of classification is apparent in two of the most famous aspects of Linnaean taxonomy, the binary system of nomenclature and the sexual system. Binary nomenclature was, as Linnaeus quickly realised, an ideal system for easily applying a name to a group of plants. "As easily as one names a person", is how Linnaeus himself described its use (quoted in Stafleu 1971: 109). The sexual system, with its emphasis on such easily discernible features of plants as the numbers of stamens and pistils, allowed any new plant species to be rapidly incorporated within the categories of the system.

As Stafleu (1971: 143-339) points out, in a valuable appraisal of the reception of Linnaean taxonomy, it was the practical utility of his methods which so attracted eighteenth-century botanists and which largely accounts for the enormous success of Linnaean taxonomy in the years which followed Linnaeus' death. Descriptions were standardised, names given according precise rules, a classification was made possible which allowed accurate storage and retrieval of large amounts of taxonomic information. The practical value of the system was especially evident in Britain, where it served the needs of an expanding empire in ordering a flood of exotic new plant materials which had scientific, medical and horticultural importance. In addition, its assumption that species were distinct entities held together by continuous generation and separated by essential differences, accorded well with the Biblical account of species and their origin, an account still prevalent when Linnaeus was writing, and a view to which he himself largely subscribed.¹

In very broad and general terms, the developments which were to lead to the emergence of experimental taxonomy or biosystematics can be

1. In his later life Linnaeus argued that it was the genera which were created in the beginning and that these were subsequently blended to form the species. However, even here the overall framework of belief remains Creationist and there are no grounds for seeing Linnaeus as a forerunner of transformationist doctrines.

traced to a reaction against Linnaean taxonomy. This reaction was confined at first mainly to middle Europe and, more particularly, to eighteenth-century Germany and France. And it was a reaction led by men who were not, primarily at least, taxonomists but rather experimental biologists.

Of the German botanists, Joseph Gottlieb Kölreuter (1733-1806) and Joseph Gaertner (1732-1791) are the two whose names have most often been linked with the emergence of experimental taxonomy.² Indeed, Kölreuter's experiments in plant hybridization have been described (Olby 1966: 21) as the starting point for the science of experimental genetics. Kölreuter did not believe that hybridization could produce new species in nature, but later biosystematists (e.g. Clausen, Keck and Hiesey 1939: 103; Clausen 1962: 5) have seen in Kölreuter's observations the first experimental evidence both for hybridization and for the existence in nature of interspecific barriers to gene-exchange. Joseph Gaertner was a personal friend of Kölreuter and is best known for his anatomical and morphological studies of seeds and fruits. He was the first botanist to recognise endosperm³ and among the first to use the term 'embryo' to describe the young plant within the seed (Stafleu 1971: 257-259). His son, Carl Friedrich von Gaertner (1722-1850) performed hybridization experiments and Olby (1966: 39) describes the latter's work as being in direct succession to Kölreuter's and a direct precursor of Mendel's experiments.

The contributions made by the biologists of the French Enlightenment to later developments within taxonomy were more nebulous, but not necessarily of less importance. In very different ways this topic is considered by Stafleu (1971: 267-339), Foucault (1970: 217-249) and Schiller (1974). Schiller emphasises the increasing importance of experimentation to the late eighteenth-century biologists, a concern which he sees in part as a reaction against the previously excessive

2. Other eighteenth-century botanists could undoubtedly be added to this list. For example, Stafleu (1971: 247) also sees the Swiss botanist Albrecht von Haller as an early advocate of biosystematical doctrines.

3. Endosperm is the nutritive tissue which surrounds and nourishes the embryo in seed plants.

concerns with classification. Both Foucault and Stafleu stress the increasing importance of time in an understanding of biological phenomena. This new awareness of time results in a strong temptation to see in the work of figures such as Buffon and Lamarck anticipations of the later developments which were to occur during the nineteenth and twentieth centuries. However, the dangers of overemphasising such parallels is well brought out by Bowler (1974). As he shows, late nineteenth-century evolutionary theories were remarkable in two respects: in their dynamic treatment of nature and natural phenomena, and in their abandonment of the idea that the universe was created or planned by an intelligent Creator. Enlightenment thinkers such as Buffon and Lamarck certainly held to a more dynamic view of nature than had their predecessors, but their thinking, even when "evolutionary" or "progressive", remained within an overall framework which was usually Creationist in at least some of its aspects.⁴

Within taxonomy itself the period of some eight decades between the death of Linnaeus and the publication of Darwin's Origin of Species saw many developments and refinements of concept and practice, albeit within an essentially Linnaean framework. Linnaean nomenclature reforms eventually gained a nearly universal acceptance and those (e.g. Adanson) who chose not to use them found their work isolated and ignored as a consequence. There was a continuation of the search for a 'natural system' of classification and, towards this end, more and more characters, including some internal characters, came to be deployed by taxonomists. In zoological taxonomy larval forms became an increasingly important source of new information (Winsor 1976) and the development of new and better microscopes greatly facilitated this process. However, classifications continued to be based broadly upon resemblances of form and taxonomists still directed their attention primarily to the description of differences between species rather than to an analysis of variation within the species.

By the second half of the nineteenth-century one of the two plans on which the success of Linnaean taxonomy was based appeared to have

4. Interestingly, as Bowler shows, the enlightenment thinkers who came closest to anticipating later evolutionists were not atheists but deists. Any simple portrayal of evolutionism as a reaction against Christianity is therefore to be avoided.

been finally removed from biological thought. If gradual transformation of species occurred, then species could not be the fixed, unchanging entities which they had previously been thought to be. Indeed, if the Darwinian account of gradual speciation was accepted, then the very existence of species as previously conceived was thrown into doubt. Darwin himself ascribed to a nominalistic species concept; for Darwin species were abstractions, fictions of the taxonomist's mind rather than objectively existing entities in nature:

Hereafter we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate graduations, whereas species were formerly thus connected ... It is quite possible that forms now generally acknowledged to be merely varieties may hereafter be thought worthy of specific names ... In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect, but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species.

(Darwin 1859: 460)

In retrospect, especially if one views progress in science purely in terms of the history of ideas, it is hard to see why the acceptance of Darwinian evolution in the latter half of the nineteenth-century did not precipitate a crisis in taxonomy. In terms of its logic the threat posed by Darwinian natural selection to a Linnaean-based taxonomy is not difficult to grasp. If it is accepted that the only basis for a natural classification is evolutionary theory and that species develop gradually, and, if change from one species to another is too gradual to be able to delimit them, clearly species cannot be defined or delineated in the classical manner. As Heslop-Harrison (1953: 8-9) says, "the idea of organic evolution was in several ways in conflict with the practices of orthodox taxonomy from the beginning ... Darwin's doctrine was implacably opposed to such an interpretation of natural variation."

However, as a number of later authors have pointed out (e.g. Davis and Heywood 1963: 31-33; Heslop-Harrison 1953: 11), the acceptance of the Darwinian thesis of evolution through natural selection had remarkably little effect on the actual practice of taxonomy during the

years which followed its acceptance by the majority of the biological community. The theory of evolution, while it provided a new framework within which the existence of classifications could be interpreted, did not actually provide any new techniques by which such classifications could be produced. The aims of herbarium taxonomy remained to find and describe new species and to provide a framework in which the diversity of living organisms could be described and ordered. The existence of such order could now be given an evolutionary or phylogenetic interpretation; organisms were seen as related through descent, but the methods used for producing such classifications remained much as before.

Thus, rather than overthrowing the structure of nineteenth-century taxonomy, evolutionary theory actually came to provide a source of support for the existing methods. The Linnaean system, with its ordered hierarchy of categories, was seen as a demonstrable proof of the affinities between organisms postulated by the evolutionary hypothesis. It is true that the acceptance of evolutionary speciation cast doubt upon the real existence of species as the fixed unchanging entities which had been posited previously, but taxonomists were often quite willing to accept that there was a 'subjective' element to species-making. To make such an admission was not, in itself, a threat to traditional taxonomic practice. Species might indeed be nominalistic; they might indeed be creations of the taxonomist's mind, rather than objective realities, but, if they were a fiction, they were a convenient and indeed necessary one.

The writings of the American taxonomist Lynn Bailey (1896) illustrate this point particularly well. Bailey admitted that, given evolution, the species of the early naturalists like Linnaeus were not objective entities but creations of the taxonomist's mind. However, he did not advocate either the abandonment of Linnaean methods or the Linnaean system. Indeed, he argued that it is precisely because species are only a convenient fiction that an approach to species-making based on external morphology is to be desired. Species thus become defined in purely pragmatic terms as a "unit of classification, designating an assemblage of organisms which, in the judgement of the writer, is so marked and so homogenous that it can be conveniently spoken of as one thing" (Bailey 1896: 457).

Thus, the situation in 1900 was that orthodox taxonomy had seen little change either in its aims or methods since the time of Linnaeus. The aim of classification remained to describe new species on the basis of resemblance of morphology, or form, and thus to impose order on the immense variety of natural kinds. The herbarium remained the focal point of taxonomic enquiry. Linnaean categories, with additions where necessary, remained in use and indeed have continued to find employment up until the present day. The Linnaean method, by and large, continued to be perceived as appropriate for the job at hand. As Heslop-Harrison (1953: 10) comments:

... during the century-and-a-half after Linnaeus the taxonomic methods which he had so largely helped to establish were successfully employed with little or no modification to complete a major part of what might be termed the primary survey of the higher groups of the plant kingdom. Order was imposed where order had not been before, and to this extent the aims of classical taxonomy were achieved.

And Simpson (1961: 63-64) has argued that zoological systematics at the turn of the century was in a similar position.

The lack of any intellectual crises within taxonomy is borne out by the proceedings of a symposium on the species question initiated by Henry Bernard in 1900. Bernard was a zoological systematist who was working on a catalogue of corals then being prepared by the British Museum of Natural History in London.⁵ The evidence about this symposium's discussions comes from correspondence found in the papers of William Bateson. These letters were written to Bernard from the leading biologists and naturalists in Britain, including E. Ray-Lankester, W.C. Thiselton-Dyer, W.F.R. Weldon, D. Sharp, A.R. Wallace, and Bateson himself. The symposium's main concern was with the value of Linnaean nomenclature in groups, like the corals, where very little evidence on morphology and variation was available. Bernard had found great difficulty in his own work in applying Linnaean nomenclature and methods of such instances. However, the most striking feature of the symposium was the almost unanimous agreement that the

5. This symposium and the general light it sheds on biology in Britain at the turn of the century is discussed in a recent paper by Cock (1977).

Linnaean species, based on morphological discontinuity of form, could be the basis for a permanent and adequate taxonomy, provided that sufficient material of the species was available and that the taxonomist was competent at his task. Of the contributors to the meeting only Bateson offered any dissension on this point.⁶

However, although there was little awareness from within the taxonomic community of any need to radically alter their objectives or techniques, there was, towards the end of the nineteenth century, increasing hostility towards traditional taxonomy from other branches of biology. This hostility was initially concerned as much with the methods employed by orthodox taxonomy as with the results that were being obtained. Within botany at least, this enmity of taxonomy can be traced back to the emergence of physiological botany during the second half of the nineteenth century.

As Coleman (1971) has shown, biology in the last half of the nineteenth century was becoming an increasingly experimental science. Experimental methods had entered botany via the work of German physiologists of whom Julius Sachs (1832-1897) was the outstanding figure. Sachs became a leading advocate both of the new experimental methods and of the reductionist philosophy with which they were associated. For the new physiologists plants and animals were machines, whose functioning could be explained in terms of physical and chemical laws. Amongst Sachs' pupils at Würzburg was Hugo de Vries (1848-1935), who was later to become one of the co-discoverers of Mendel's work and an early advocate of an experimental approach to the species problem.

In Britain the "New Botany" was chiefly associated with the work of T.H. Huxley, W.T. Thiselton-Dyer, S.H. Vines, H. Marshall Ward and F.O. Boyer.⁷ Of these, Huxley especially was a vigorous champion of the new physiology: more interested in form and function than in classification, he found little need for systematics in his work:

6. Bateson argued that great changes would be made in systematics in the near future, although he did not elucidate the direction in which he believed that these changes would proceed.

7. A discussion of the work of all these figures and their role in the emergence of the "new botany" in Britain is given in Bowyer's (1938) autobiography.

The only part of my professional course which really and deeply interested me was physiology... I am afraid there is very little of the genuine naturalist in me. I never collected anything and species work was always a burden to me.

(Huxley, quoted in de Beer, 1974: 102)

And Huxley was convinced that experimental methods were vital to biology:

... physiology is the experimental science par excellence of all sciences; that in which there is least to be learnt by mere observation, and that which affords the greatest field for the exercises of those faculties which characterise the experimental philosopher.

(Huxley 1854, quoted in Bibby 1967: 54)

However, in Britain at least, the "New Botany" made slow headway against the already established systematics. Bowyer (1938: 26) suggests that a reason for this resistance can be found in social and economic conditions prevalent in Britain in the 1870's and 80's. The expansion of Imperial interests in Victorian Britain had led botanists to concentrate on floristic and taxonomic studies of the British dependencies to the exclusion of laboratory botany:

I remember about 1876 how I longed for a train of wagons to convey the Cambridge herbarium away to Kew, and so to vacate for the new botany the rooms that would have served its needs. A crude idea no doubt, but it reflected the inverted narrowness of outlook which the time had imposed upon us.

(Bowyer 1938: 102)

The tensions between the old established systematics and the "new botany" erupted in the so-called "war" between physiologists and taxonomists which took place in the 1880's and 1890's.⁸ It was a "war" which taxonomy was ultimately destined to lose. In 1884, Hooker, writing to a friend concerning an appointment of a vacant chair of botany in an English university, felt need to give the warning that:

Botany is no longer a knowledge of plants, but how plants 'come about' and what they do! ... There is no question of the high scientific value and interest of all this, but the outcome of years of it may leave a man in utter ignorance of any plant bigger than the Torula or Mucor he began with ...

8. Much more historical research is required to elucidate the reasons behind this controversy. A brief discussion of its consequences for amateur natural history in Britain is given in D.E. Allen (1976: 176-194).

Botany of this sort is the study of the laws of life, the highest of any: but to pursue it requires a special education; and to teach it a special practice; and I do not know if you have had either. I have not ... Our careers are very different from this, and you are making your mark in yours, would it not be better to stick to it? Or only leave it for something in the same line?

(Hooker 1884, quoted in Huxley 1918: 403-404)

And Hooker was not alone in making such a gloomy prognosis; in the years which followed other established British taxonomists such as Charles Babington and Alfred Newton were to echo these sentiments. The comparatively modest status of taxonomy by the turn of the century is reflected accurately in Sir Joshua Reynold Green's A History of Botany (1909). Taxonomy is accorded merely 22 pages. Anatomy and physiology are given a 370-page treatment, much of it, as the author acknowledged, concerned with research of quite recent origin.

However, the controversy between experimental botanists and systematists was not one which was entirely confined to matters of relative importance and status. Darwin's work had reemphasised the importance of the concept of "species" to all biologists, whether they were concerned with taxonomy, evolutionary theory or mechanisms of physiology and heredity. Also, Darwin's work initiated a long controversy concerning the mechanism of speciation. Darwin had suggested that evolution took place primarily through the action of natural selection on small, essentially continuous variation. Another possibility, and one not completely ruled out by Darwin, was that the environment could act directly to produce new species (a view which became attributed to Lamarck). Still another possibility, and one favoured by Huxley, was that new species could arise by sudden "leaps" or "saltations". Which of these mechanisms was correct and what exactly was a species anyway? Amongst experimental biologists at the turn of the century there were some who felt that the problems concerning the nature of the species and its origins were too important to be left to the hands of descriptive naturalists and systematists. It was at the hands of these figures that the first attempts to construct an "experimental taxonomy" were made.

Attempts to solve the species problem by experiment

1. Transplant Studies Prior to 1920 A number of nineteenth-century

botanists used transplant studies in an attempt to obtain experimental evidence about speciation. Three figures merit special attention because their work was taken up and developed by later experimentalists: Alexis Jordan (1814-1897), Anton Kerner von Marilaun (1831-1898) and Gaston Bonnier (1853-1923).⁹

Alexis Jordan was a French botanist, born in Lyons and author of, inter alia, Observations sur plusieurs plantes rares (1846); De l'origine des diverses varietes ou especes d'arbres cultives (1853) and the Icones ad floram Europae (1866). Jordan took plants belonging to different varieties of the same Linnaean species and demonstrated that, even when transplanted into the same standard garden at Lyons, these plants remained distinct and different in their morphological features. He concluded from this that these so-called varieties must, in fact, be species. Clausen (1962: 5) credits Jordan with the discovery of local populations within the Linnaean species although, as Clausen admits, Jordan did not interpret his results in this way. Jordan's views were revived in modified form by some geneticists and ecologists in the period after the rediscovery of Mendel's work in 1900. Clausen, Keck and Hiesey (1939: 103) suggest that the very narrow interpretation of the species promoted by Jordan, and by later figures such as Lotsy and Cockayne, was a factor in the unfavourable reception of experimental taxonomy by orthodox taxonomists at the beginning of the twentieth century, although they produce no evidence to back this claim.

Anton Ritter Kerner von Marilaun was born at Mautern, lower Austria, and became professor of botany at Innsbruck and Vienna. Kerner was an important figure for the later experimental taxonomists because he carried out the first transplant experiments of the varied-environment type. He established two alpine gardens in the Tyrolese Alps - one at 2195m and a second at 1215m. These, together with his two lowland gardens at Innsbruck (569m) and Vienna (180m), provided the location for a series of experimental transplantations of plant species from lowland to alpine habitats and vice versa. The

9. Little historical work has been done on Jordan, Kerner or Bonnier. The account which follows is taken mainly from the writings of later experimentalists and especially Jens Clausen (see Clausen 1962, Clausen, Keck and Hiesey 1939, 1940). Jordan especially would repay closer attention by historians of twentieth-century biology because his species concept was important not only for later developments in biosystematics but in general genetics as well.

results of these experiments were published in the monumental Pflanzenleben (1891, vol. 2, pp. 249-507). A major object of the research had been to determine whether environmentally induced variations in plant growth could become inherited. Kerner did not, himself, rule out such a possibility. However, his results, given a modern interpretation, can be seen as evidence against this hypothesis (cf. Clausen, Keck and Hiesey 1940: 394-396).

The same interpretation cannot be placed on the work of the French botanist and plant physiologist Gaston Bonnier, who in the late 1880's and 1890's was professor of botany at the University in Paris. Bonnier's transplant experiments were carried out in the Pyrenees and Alps from 1886 to 1889, although the full account of the results obtained was not published until 1920 (cf. Bonnier 1890, 1895, 1920).

Bonnier concluded from his experiments that one species could be transformed into another by the action of external environmental influences such as changes in light, temperature and humidity. Amongst the examples he gives of such transformations are the evolution of lowland Helianthus vulgare into H. grandiflorum; of lowland Silene nutans into alpine S. spathulaefolia and of Lotus corniculatus into L. alpinus. These conversions occurred over long periods of time, sometimes as long as 30 years, and Bonnier found that the opposite effect - the conversion of alpine into lowland species, was difficult to achieve.

Bonnier's work became important for later experimental taxonomists who also held that environment could bring about species transformation. Clements, in particular, became an ardent supporter of Bonnier's work. However, supporters of selectionist theories of evolution found his results puzzling. Clausen, Keck and Hiesey (1940: 396-401) argue that Bonnier was led into error by inadequate methodology; and that he mistook weeds which had contaminated his experimental gardens for transformed species. This is an explanation which is plausible given that Bonnier found, as a general rule, that species transformations only took place where the lowland forms were transplanted to a region where the alpine species grew naturally. Bonnier kept no herbarium specimens and his only recorded observations were in the form of notes,

so that it is also possible that he made inexact comparisons between lowland and alpine specimens. Clausen et al. end their discussion of Bonnier's experiments with, "the hope that a repetition of his work, using the same species in the same region under carefully controlled conditions, may be stimulated" (1940: 401). However, this task has never been undertaken.

2. Hugo de Vries and the mutation theory

Studies of ecological transplants were not the only techniques being used by experimental biologists at around the turn of the century to put the species "question" on an experimental base. After the rediscovery of Mendel's work in 1900 and the subsequent emergence of the new discipline of genetics, plant hybridization also came to be seen as an important technique for experimental investigations. This point is well illustrated in the work of one of the rediscoverers of Mendelism, Hugo de Vries.

A physiologist by training, De Vries championed a new, and for a time, highly successful, theory of speciation. In his Die Mutationstheorie, published in English as The Mutation Theory, De Vries (1910-11) argued that species originated not through the action of selection on small, continuous or fluctuating variation, as had been maintained by Darwin, but by large scale mutations, saltations or leaps. The claim, moreover, was made that these mutations could be studied experimentally, and De Vries himself conducted experiments to test his theory, mainly on the plant genus Oenothera.¹⁰

For De Vries mutation itself was a process which took place in two steps (De Vries 1910-11, ii: 56-75). The first of these was the production within the genetic material (pangenes) of a new "unit of character". To this process, De Vries gave the name premutation. The second step which was a physiological process, involved the activation of the new genetic material to produce a new character in the phenotype of the plant. This latter process led to the actual mutation observed in the plant. From this basis, De Vries was able to conclude that mutations were of three types, viz.: 1. Progressive,

10. In the passages which follow quotations are taken from the English edition of Die Mutationstheorie translated by J.B. Farmer and A.D. Darbishire.

2. retrogressive, 3. degressive.

Progressive mutations were the only ones which involved the actual creation of new genetic material, i.e. premutation. Retrogressive mutations occurred when a genetic unit (pangene) present in the plant became, for reasons which were unknown, latent or inactive.

Degressive mutations occurred when, again for reasons which were unknown, a pangene which had been inactive for a period of time became re-activated. Retrogressive and degressive mutations (and hybridization) involved, therefore, new permutations of active genetic material. But, progressive mutation involved the actual creation of new genetic material.

As Garland Allen (1969) has shown, in a valuable account of the reception of the mutation theory, there were many factors responsible for its initial success. Important amongst these were the weaknesses in its great rival, the selectionist theory of the Darwinists. In 1900, many biologists, while they could accept that selection acted as a sieve to "weed out" or eliminate unfavourable variation, could not understand how selection actually leads to the origin of new species. De Vries had used this argument and in the period just after the publication of The Mutationstheorie his views were given striking corroboration by the Danish plant geneticist Wilhelm Johannsen (1857-1927).¹¹ Johannsen was concerned with studying pure lines, i.e. all the individuals which are descended from a single individual by self-fertilization. Using a plant species which can be self-fertilized Johannsen tried to select over several generations for characters such as overall length, breadth and weight. The object of these experiments was to determine if Darwin or De Vries was right, i.e. whether selection could act on continuous variation almost indefinitely or if selection of continuous variation was ineffective beyond certain limits. His conclusion was that, in pure lines at least, there was no experimental evidence that selection could lead to the appearance of new characters:

11. Johannsen's contributions to genetics are discussed in a recent paper by Nils Roll-Hansen (1978). As Roll-Hansen shows there was close liaison between Johannsen and Hugo de Vries. De Vries believed that pure lines were elementary species and Johannsen agreed that the two were equivalent, at least in theory (Roll-Hansen 1978: 215).

... the action of selection cannot be carried out beyond fixed limits - it must indeed cease when the purification, the isolation of the particular most strongly deviating line, practically speaking, is carried out to completion.

(Johannsen 1903, quoted in Provine 1971: 94)

The assumptions of Johannsen's work were immediately challenged by neo-Darwinists such as Pearson, Weldon and Yule. However, experimentalists acclaimed the research; for them it was an exciting new theory, opening up new avenues of research and firmly based upon experimental evidence.

There were other reasons for the success of the mutation theory. It appeared to be able to deal with the then widely-held doctrines of orthogenesis or progressive evolution in a way which was better than its rival theories.¹² Opponents of neo-Lamarckianism were attracted to the theory because De Vries included environmentally-induced variation under his category of those "fluctuating variations" which cannot lead to new species. Similarly, opponents of the biometricians, such as Bateson, saw in the work of De Vries a refutation of the doctrines of eugenics.¹³ The theory solved (by denying its importance) the controversy surrounding the question of what role isolation played in speciation. Even Lord Kelvin's claim, based on thermodynamical calculations of the activity of the Sun, that the Earth could not be old enough for evolution to have taken place was partially solved by the mutation theory; mutation is a faster process than gradual speciation.

12. Allen (1969: 77) puts this point in the following terms:

To those biologists who held a belief in some sort of directionality to evolution, de Vries offered a handy explanation which did not resort to teleological implications of orthogenesis. In Darwinian terms, minute individual differences, occurring by chance, might never have become established because of swamping or because they were not initially useful. De Vriesian mutations, on the other hand, were definite, and directional from the start, providing a foundation on which further mutations could build.

13. Indeed de Vries himself stated that if his view of speciation was correct then the question of the origin of species could be one which had no bearing on the solution of social problems (see de Vries 1910-11, i, 154-159 and 213).

However, as Allen (1969: 79-85) rightly emphasises, the major attraction of the theory for most biologists was that it appeared to set the whole problem of what a species was and how new species could be formed upon an experimental base. To see how this was the case we must examine further De Vries' conception of the species and how it related to his evolutionary doctrines discussed above.

The starting point of De Vries' species concept was the denial that the so-called "species" of the systematist have any objective or real existence in nature. The only "species" which could even be considered as being real or objective entities were "elementary species". And by "elementary species" De Vries meant species in the Jordanian sense, that is, forms which bred true under cultivation:

Whilst we may hope that the origin of new elementary species will one day become the subject of direct investigation, we must be perfectly clear as to the essential difference between these and the so-called Linnaean species which are (usually) groups of elementary species. An elementary species can be identified in any given case by the test of cultivation; how many such forms should be united to one Linnaean species is a matter for so-called taxonomic instinct, just as is the settlement of the limits of genera and families.

... Linnaean species are collective and artificial whilst Jordan's species are single and real.

(De Vries 1910-11, i: 58, 171)

However, De Vries did not have a conception of the species which was the same as that of Jordan. The reason why he had a different view is linked to his theories about mutation and is discussed at length in volume two of The Mutation Theory (1910-11, ii: 567-598). Thus, for De Vries, mutations could be progressive, retrogressive or degressive. But, only progressive mutations are based on the addition of actual new genetic material and only progressive mutations lead to speciation. Retrogressive and degressive mutations lead to the origin of new varieties, but these varieties will also breed true under cultivation. Hence the question becomes: how do we recognise the real elementary species from retrogressive and degressive mutations which give the appearance of being new species, but which in fact are not based on premutation, and are only varieties?

The answer is that we can do so by means of Mendelian genetics.

Forms which have arisen by retrogressive and degressive mutation, because their pangenes are still present (even if, as in the case of retrogressive mutations, inactive), will obey simple Mendelian laws when hybridized. But, where a genuine addition has been made to the genetic material, hybridization will result in non-Mendelian ratios in the F_2 and subsequent generations. De Vries called a cross of this sort a unisexual cross:¹⁴

Mendelian hybrids correspond to retrogressive and degressive specific differentiation, and consequently to true varieties; unisexual hybridizations correspond to progressive specific differentiation and consequently to elementary species.

(De Vries 1910-11, ii: 584)

Thus, for De Vries, both tests of experimental cultivation and hybridization experiments were needed in order to tell what a species really was. The effort involved was worthwhile because, as De Vries constantly emphasised, if we do not know what a species is, how can we ever come to know anything about its origins?

As Allen (1969: 68-69) has shown, the demise of the mutation theory was as spectacular as its initial success. Between 1910 and 1912 Bradley-Davis showed that Oenothera, on which De Vries had based most of his research, had an unusual hereditary system but that, nonetheless, the hybrids which could be made obeyed Mendelian laws. In 1914 Renner showed that Oenothera was a permanent heterozygote; and in a long series of publications, starting in 1923, R.E. Cleland showed that the "mutations" in Oenothera were explicable as being due to a complex series of chromosomal translocations.¹⁵ Allen concludes that the mutation-theory of De Vries was already in serious trouble by 1915, and by the early 1930's the theory had been abandoned.

However, the significance of the theory to our own concerns

14. Why de Vries uses the term "unisexual" here is not made clear. Presumably it is because the new pangenes is only present in one of the plants (either the male or female) used in the crossing experiment.

15. The details of this research are complex and will not be elaborated here. The best introductory account to modern research on Oenothera genetics is that contained in Stebbins (1971).

should be clear. It shows that experimental biologists in 1900 were profoundly dissatisfied with the species of traditional systematics, and that they were, moreover, actively seeking alternatives. De Vries was well aware of the practical problems which his notion of species raised for traditional taxonomy. However, in the long run at least, he believed that there were practical difficulties which would have to be overcome:

Numerous experiments in hybridization are necessary before they can serve as a foundation for systematic distinctions. But the leading principle in these researches must always be the attempt to determine the elementary characters.

(De Vries 1910-11, ii: 589)

3. J.P. Lotsy and the Hybridization Theory

Jan Paulus Lotsy (1867-1931) has a strong claim to be regarded as the first taxonomist to explicitly advocate the formation of a new discipline of experimental taxonomy. He was born at Dordrecht and educated at the University of Gottingen. A physiologist and taxonomist by training Lotsy had become interested in the possibilities of linking taxonomic studies with the new field of genetics from as early as 1903.¹⁶ However, it was only in 1909, after his resignation from the University of Leiden, that Lotsy was able to set up the experimental gardens needed for such a project, at Haarlem and later at Velp.

Lotsy's work encompassed similar concerns to those of De Vries, although they were elaborated within the context of a very different theory of evolution. The starting point of Lotsy's work is the claim that in order to understand evolution we must know what a species is: "he who ventures to write on the origin of species, ought to define what a species is" (Lotsy 1916: 13).

Systematists have failed in this task. Their species, which Lotsy calls Linneons, are arbitrary units definable only on morphological grounds:

16. For an obituary on Lotsy (in Dutch) and a complete list of his research publications see Goddijn (1931).

The Linnaean species is no species ... A Linneon (is) the total of individuals which resemble one another more than they do any other individuals.

(Lotsy 1916: 22)

Within these Linneons can be found forms which remain constant when cultivated under uniform conditions. These are the elementary species of Jordan. However, for Lotsy breeding true to type under conditions of cultivation is not a test of specific purity. He argues this because, like De Vries, Lotsy held (1916: 22-23) that only hybridization experiments could determine real species. Thus, the elementary species of Jordan are in fact not species but Jordanons and are defined as

a group of externally alike individuals which all propagate their kind faithfully, under conditions excluding contamination by crossing with individuals belonging to other groups, as far as these external characters are concerned, with the only exception of non-inheritable modifications of these characters, caused by the influences of the surroundings in the widest sense, to which these individuals or those composing the progeny may be exposed.

(Lotsy 1916: 27)

To establish a genuine species, neither morphological comparison alone or experimental cultivation alone will suffice; hybrid analysis is required as well. And species for Lotsy (1916: 27) are defined in purely genetical terms as, "a group of individuals of identical constitution, unable to form more than one kind of gametes; all monogametic individuals of identical constitution consequently belong to one species".

A consequence of this is that not all individuals belong to a species. Many individuals can produce more than one type of gamete. These heterozygotes are not species but hybrids. Thus hybrids are:

... all individuals able to produce more than one kind of gametes, e.g. gametes of different constitutions ... Hybrids consequently are polygametic.

(Lotsy 1916: 28)

The final category which Lotsy introduces is the modification. This term designates forms which have become different through the external effect of environment but these differences are not inherited. Thus a modification refers to "the non-transmittable effect of external circumstances". (1916: 28)

This hierarchy of categories is radically different from that used by traditional systematists. For traditional systematists there are: 1. Species (in the Linnaean sense); 2. Subspecies; 3. Varieties all defined on morphological grounds. For Lotsy there are: 1. Linneons; 2. Jordanons; 3. Species and hybrids; 4. Modifications and only one of these categories (the Linneon) is definable in terms of pure morphology alone.¹⁷ To determine the other categories of the system require either hybrid analysis, or tests of cultivation, or both.

Lotsy's evolutionary views stem from this system of classification and, in particular, from his definition of the species. Species are gametically pure and hence do not possess any variability (Lotsy 1916: 29-41). The apparent variability of species is caused by their frequent hybridization. An important question which follows is whether there is any other mechanism (i.e. other than crossing) by which pure species (which are homozygous) can become heterozygous. If such a mechanism did exist then this would be a mutation in Lotsy's use of that term. But, Lotsy argued, although this kind of process is a possibility, it has never been demonstrated experimentally, even in Oenothera. For the "species" which De Vries studied were not species but hybrids:

De Vries has shown that O. lamarckiana is a heterozygote and he has shown nothing else; all the rest is mere hypothesis.

(Lotsy 1916: 32; italics in original)

Thus, both the Darwinists and De Vries are, according to Lotsy, wrong. The Darwinists are in error because true species are not variable; De Vries is wrong because mutation is not an experimentally proven fact but an unproven hypothesis. Neo-Lamarckians can be similarly dealt with. That environment may cause changes in the genetical material (i.e. mutations) is possible, but again is an experimentally unproven hypothesis. And in all likelihood, therefore, inheritable variability does not exist.

Having thus disposed of his rivals, Lotsy was able to construct

17. Lotsy was aware that capacity to breed freely and produce fertile offspring was also a criterion by which members of the same Linneon might be recognised. However, Lotsy maintained that inter-Linneotic crossings sometimes took place. Indeed it was through such crosses in the past, Lotsy argued, that higher taxa such as classes and orders had been derived.

an alternative account of evolution (Lotsy 1916: 42-95). For Lotsy the primary problem of evolution was not how species arose, for pure species are now rarely found in nature, and may have arisen at some point in the long distant past from inorganic matter. Rather, the problem was how these pure species give rise to the subsequent bewildering variety of natural kinds. A chemical analogy is used to make this clear:

The problem of the species and of its origin is consequently comparable to that of its pure chemical substance and its origin, the problem of the heterozygotes of different constitutions which we find in nature and of their origin is comparable to the problem of ores found in nature and their origin. Just as we don't study the origin of pure chemical substances in nature, but investigate this origin in the laboratory, so the question of the origin of species cannot be tackled in the field, but must be studied in the experiment garden.

(Lotsy 1916: 42, 53)

For Lotsy, hybridization provided the only experimentally proven mechanism whereby new forms can arise in nature. Species, in the Lotsyan sense will, when crossed, produce polygametic forms. These polygametic hybrids are, in turn, able to produce new individuals, some of which are heterozygous, but some of which are homozygous, i.e. new species. We can isolate such homozygotes experimentally and multiply them by self-fertilization, or by fertilization with individuals of identical genetical constitution. However, if random-mating occurs, then the proportion of species to hybrids will not change. The only role which selection played in this process was the extermination of some of the new species or hybrids which have been produced. Selection is only another name for extinction, the last forms to disappear being the "selected ones".

The Vera Causa of the production of new types consequently is: crossing; the vera causa of their extinction: the struggle for life; the selection resulting from the latter, is by no means a revival, but is the sign of struggle of the doomed.

(Lotsy 1916: 160)

Lotsy never altered his evolutionary views, as his later writings demonstrate (Lotsy 1925, 1927). His experimental hierarchy of Linneons, Jordanons, species, hybrids and modifications did not become popular with subsequent experimental taxonomists. It was

based on a theory of evolution and speciation which was not accepted by later experimentalists, who were either neo-Lamarckians or selectionists. However, the work of Lotsy, like that of De Vries, shows that geneticists at the turn of the century were actively trying to formulate an experimental conception of the species which would be of value in dealing with questions concerning heredity and evolution. And, inasmuch as this was the case, their objectives were shared by later biosystematists, even though the evolutionary conclusions which they drew from their work were refuted.

Discussion: Essentialist Strategies of Classification in the Work of Linnaeus, Jordan and Lotsy

It will be pertinent here to review the basic tenets of Putnam's theory of classification. Those tenets are

1. That the classification of natural kinds depends not upon identifying descriptions but upon the discovery of essential properties or relationships.
2. That these essences are usually to be found in the hidden microstructure.
3. That the extension of a term is derived not from an identifying description (intension) but from "paradigm" or "candidate" instances. Thus, the first instance of a term christens its usage. Subsequent instances bear a same-essence relation to the initial instance. As a result, natural kind terms are, like proper names, indexical expressions: they are used as rigid designators.

Because Linnaeus used morphological characters to define species his mode of classification appears to be superficially of a descriptive kind. However because Linnaeus held these external properties to be the essence of a species, there are also many parallels to be found with Putnam's theory of classification.

These parallels are located partly at the level of general analogy. However the similarities are more specific than this. Linnaean taxonomy, in practice, assumed a form which is very close to Putnam's predictions of how scientific classification should be achieved. For Linnaeus all the members of a single species were indeed possessed

of an essential identity of same-essence. Once these essential features had been described for one member of a new species they were known for all members - hence the overwhelming importance of the type specimen in Linnaean taxonomy. What assumptions make this a good strategy for classification. Basically there are three crucial assumptions:

1. That for any species some morphological properties are essential, i.e. they will be found in all members of that species but not in members of other related species.

2. That these characters are fixed, permanent and never change. In other words species retain these characters, they breed true within the limits of their own kind.

3. That anything which does not breed true within the limits of its own kind is not, ipso facto, a true species.

Assumption 3 is critical in understanding the distinction in Linnaean taxonomy between species and varieties. A variety of a species differs from the typical member in properties which are non-essential. Moreover, it was a tenet of Linnaean systematics that varieties would not breed true but revert back to form in subsequent generations:

Linnaeus drew the wrong conclusion from the phenomenon of variation: he considered it absolutely unimportant. In his opinions varieties are all what is now called phenotypic: "A variety is a plant changed by an accidental cause due to climate, soil, heat, winds, and it returns to its original state when the soil (etc.) is changed."

(Linnaeus, quoted in Stafleu 1971: 64,
emphasis added)

A consequence of this position is that, for Linnaeus, there was no conflict between a biological species concept (in terms of capacity to breed true) and a classification of species using morphological markers. Indeed it is because they breed true to form that all members of a species possess essential and unchanging morphological attributes. Varieties occur as accidents or deviations from the type. But such accidents are a superficial phenomena - in subsequent generations the variety will revert back to type and reveal, as it were, its true nature.

Jordan's work, with its emphasis on experimental cultivation of plants into a standard environment appears very "modern". Experimental taxonomists have often praised Jordan as one of the founders of their discipline. However, Jordan's work is not a radical departure from the Linnaean tradition. Jordan accepted the Linnaean distinction between species and varieties. What his work did reveal was that if breeding true to type is a criterion for designating species from varieties then many so-called Linnaean varieties must, in fact, be species. They breed true and are, therefore, good species in the Linnaean sense. Jordan's work was not a refutation of the Linnaean species concept, but rather a more correct application of those principles than Linnaeus himself ever managed to achieve.

Lotsy goes one step further along this path. In modern terms what Lotsy discovered was that two individuals of the same species, even two which look alike and "breed true", may not possess the same genetic constitution. In the parlance of modern genetics, individuals with the same phenotype may have a different genotype. However, it was an axiom of Lotsy's use of the term "species" that members of the same species always possess the same genetical constitution. A result of this axiom, when consistently applied, is that the concept of genetical variability within a species disappears altogether. Two individuals can vary but then they are not members of the same species.

Lotsy's taxonomy also fits the Putnam model. Identical genetical constitution becomes the essence of a species. Identical genetical constitution becomes the same-essence relationship which determines extension from given paradigm cases of the species in question. Lotsy did not believe in morphological essences because he knew that two individuals could look identical but have a different genetical constitution as revealed by genetic analyses. As a result his search for essences became related to hidden genetic factors instead of superficial external properties (and in this he showed a similar preference to Putnam who also seems to like his essences to be hidden from sight). However, Lotsy, like Jordan, is still working within an overall framework which derives its inspiration from Linnaeus. For Lotsy breeding true to type remains a necessary but not sufficient condition for species membership. It is not sufficient because now an even more strict criteria has been introduced: species must not

only breed true to type, they must do so because they possess an identical genetical constitution. However in its aspects of essentialism and typological approach to classification, Lotsy's work is thoroughly Linnaean. Indeed it is almost "more so". Lotsy's work is an even more thorough-going version of essentialism and rigid designation than the Linnaean system it was designed to replace.

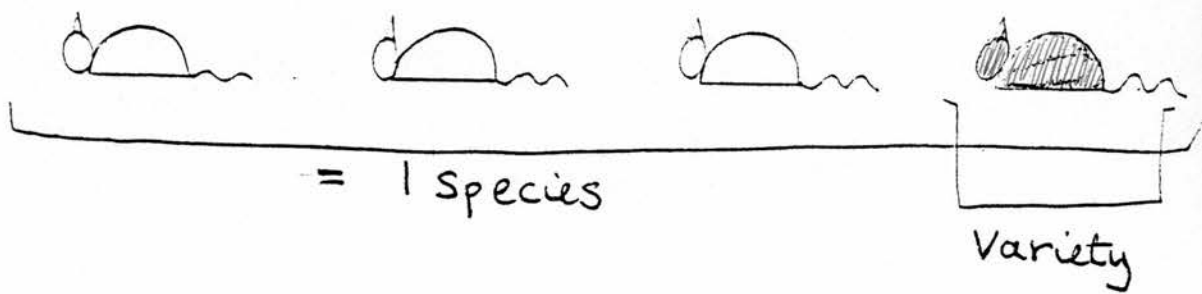
The difference between "Linnaean", "Jordanian" and "Lotsyan" taxonomy can be concretely summarised by an example which Lotsy himself discusses (cf. Lotsy 1916: 22). Thus consider a population of many white mice and a few black individuals. For the Linnaean these would probably be considered to be one species. The abnormal black mice would be varieties of which it would be assumed, reversion back to the normal white condition would be attainable if the mice were grown in the same environment.

Jordan's work shows that this assumption can be gratuitous. Black mice grown together with white mice but crossed only with black mice produce black offspring. For Jordan we have here two species.

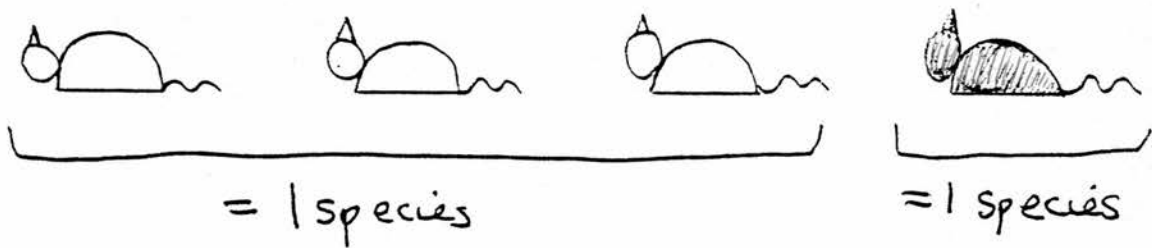
The Lotsyan taxonomists provisionally accepts this conclusion but tests it further by crossing the white mice and black mice together. When some white mice are crossed with black mice the resulting mice are white. But, in some cases different white mice are crossed with the same black mouse and the result is different viz. half the mice are white, half black. The Lotsyan conclusion is that there are indeed here two species but that not all white mice belong to that species. Some white mice are not gametically pure and must have resulted from hybrid crossing in the past between white and black mice species. Thus we have here, in addition to two species, hybrids. The resulting classification becomes a genuine reflection of the hidden genetic essences which are controlling the events which take place. These three positions are outlined diagrammatically in figure 3.1.

In terms of its formal presentation Lotsy's argument is faultless. Linnaean taxonomy stands open to the criticism that it defines species in terms of morphological characters which are simply assumed to be essential in contrast to the non-essential characters which designate varieties. Even Jordan's work can be criticised on the grounds that

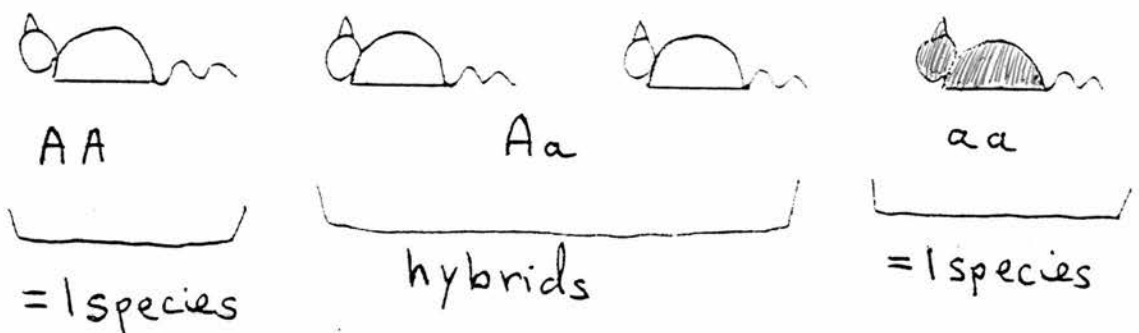
Figure 3.1. Three classifications of Mice
(for explanation see text).



LINNAEAN TAXONOMY



JORDANIAN TAXONOMY



LOTZKYAN TAXONOMY

breeding true to type does not reveal a properly essential relationship of underlying form. But Lotsy, by carrying out crosses between Jordanons, eliminates, even this possibility. A taxonomy along these lines certainly can be claimed to reveal hidden essences in the true Putnam manner. Why was it so little advocated by later taxonomists?

The reasons for this failure are complex, and cannot be more than sketched in what follows. In the case of De Vries, as we have already seen, he had the misfortune of basing most of his research on a plant genus which subsequent research showed to have an unusual and highly irregular genetic system. However, a still more important reason for the rejection of the work of Lotsy and De Vries was the increasing success of Darwinism in the period up to 1920. In 1900 the majority of experimental biologists did not believe that selection acting on small-scale, fluctuating variations could lead to speciation, by 1918 most of them did believe that such selection was the only, or at least the major, mode of speciation.

Why and how this change took place is a complex subject on which more historical research is needed (cf. Allen 1976). Provine's (1971: 90-192) account of these developments concentrates on the special importance of four figures: William Ernest Castle (1867-1962), Herman Nilsson-Ehle (1873-1949), Edward Murray East (1879-1938) and T.H. Morgan (1866-1945). W.E. Castle, working at Harvard, was a mutationist who later joined the selectionist camp. His research was concerned with the genetics of coat colour in rats and was important because it demonstrated that selection could bring about changes in characters of the phenotype beyond the limits of variation established in the original population. As Castle said (1911: 120), "I have observed characters at first feebly manifested gradually improve under selection until they become established racial traits". This work provided a refutation of the earlier claims made by those biologists, like De Vries and Johannsen, who had argued that selection was only the elimination of variability.

Equally important to the Darwinists was the work being done by H. Nilsson-Ehle, who in 1900 was an assistant to the director of the Swedish Agricultural Experiment Station at Svalof. Nilsson-Ehle, in a detailed series of experiments on the genetics of cereals, was able

to show that many cases of continuous variation in a character, hitherto considered to be unexplainable in terms of Mendelian genetics, were in fact due to complex cases of Mendelian inheritance involving not one gene but several genes controlling the same phenotypic character. From this he was able to conclude firstly, that many "mutations" were in fact due only to rare combinations of genes in a multiple-factor system, and secondly, that the primary purpose of sexual reproduction was to increase genetic variability through recombination. Little of this work was published in English, but, in America similar results and conclusions were obtained by E.M. East at the Illinois Agricultural Experiment Station where research was being conducted on maize.

The work of T.H. Morgan and the Columbia school of the "Drosophila fly room" has been considered in depth by several historians. (see especially Allen 1978). Morgan was also originally sceptical of the claim that small-scale variations could be inherited, but in the period after 1910 he and his co-workers published a mass of detailed knowledge in support of the view that "Mendelism" and "Darwinism" could be incorporated into a single account of evolution based on the selection of continuous variation.

It would seem then, that the success of Darwinism in biology had little to do initially with systematics. However, the success of the movement had a profound effect upon taxonomy. In the period before 1920 essentialist and typological approaches to the species problem were manifest. After 1920 with the acceptance not just that speciation took place, but that it was a gradual process, such strategies became much less attractive.

By 1920 the selectionists had not gained universal acceptance for their position. In particular, the idea that the environment might directly influence heredity remained in common currency until the 1930's. However, most experimental taxonomists after 1920 were Darwinists, and, as such, they denied that species could or should be conceived of as constant homogenous units. For the selectionists the fact that there was variability within the species, both in the genotype and phenotype, was not a source of embarrassment or inexactitude; rather it was a demonstrable proof that speciation took

place by selection of variation within the species. And although such a view did not lead to the removal of essentialist strategies of classification from systematics, in the period after 1920 these strategies took new forms.

Chapter Four: Experimental Taxonomy in the Period 1920-1930

Experimental taxonomy in the period before 1920 had been the province of geneticists: in the decade after it was ecologists who became most concerned with the development of experimental taxonomy. To see why this was the case it will be necessary briefly to examine certain developments in ecology at the turn of the century.

The term "oecologie" was first used by Ernst Haeckel in 1866 and in its broadest sense was taken to imply the study of living organisms in relation to their environment. However, the modern period of ecological research can be traced to two sources: the publication in 1895 of Eugen Warming's Plantesamfund: Grundtræk af den Okologiske Plantegeografi and the subsequent publication in 1898 of A.F.W. Schimper's Pflanzengeographie auf physiologischer Grundlage.¹ Tansley (1947: 130), in a discussion of the development of plant ecology in Britain, describes these two textbooks as providing "the foundations of modern ecology" and McIntosh (1976: 353) has similarly stressed their importance in the emergence of ecological thought in the United States.

As the title of both books suggests, ecology itself was a development of the older science of plant geography. However, the aims of the new science were seen as being quite different from those of its parent. Plant geographers had been concerned with floristic studies of vegetation, i.e. with recording the taxonomic species growing in any given area or locality. The new ecologists were less concerned with description and more with studying causes. The emphasis was on plants as social beings forming integrated societies. Ecologists wanted to know the factors in the environment which were responsible for causing the vegetation in any area to be what it was. Naturally, knowing what species grew in any locality was still important, but ecologists also wanted to construct classifications which were ecological rather than taxonomic.

All four concerns are well-evidenced in Warming's work. Johannes Eugenius Bulow Warming (1841-1924) was a Danish botanist, who from 1873

1. Both books were published in English: Warming's in a revised edition in 1909 and Schimper's in 1903. In the text which follows quotations are from these English editions.

to 1881 was professor of botany at Copenhagen and later (1886-1911) director of the city's botanic gardens. In the revised English edition of Plantesamfund, published in 1909, he defined the objectives of the new science of ecology as being to study:

1. The external factors affecting the plant's economy; the effects of those factors upon the external and internal structure of the plant, and upon the topographical distribution of the species ...
2. The grouping and diagnosis of the plant-communities occurring on the Earth. In connection with each class the endeavour must be made to discover the determinant factors, the modes in which they are combined, and in which they possibly may replace one another ...
3. The struggle between plant-communities.

(Warming 1909: 14)

A major feature of Warming's work was the demonstration of what we today would call adaptation. The form of every plant species is intricately related to the habitat in which it lives. Plants in deserts have succulent stems, leathery cuticles, spines and sunken stomata to prevent water loss; plants in aquatic environments have reduced xylem and root-systems and large air-spaces in the tissue; parasitic plants have special organs which adapt them to their specialised mode of nutrition, etc. Warming (1909: 2) called this phenomenon "epharmony" and defined it as the law that "every species must be in harmony, as regards both its external and internal construction with the natural conditions under which it lives; and when these undergo a change to which it cannot adapt itself, it will be expelled by other species or exterminated."²

How does such epharmony arise in nature? For Warming (1909: 369-373) this question was synonymous with the question of the origin of species. One possibility was that minor, fluctuating, or continuous variation arose spontaneously in the plant and was then selected for by the habitat. Warming was sceptical, however, that selection could explain adaptation. He noted that, "this explanation

2. The concept of adaptation or epharmony was not, of course, a new one. The adaptation of organisms to their environment had been stressed both by Darwin and by natural theologians in the nineteenth century.

has recently been assailed on many sides, and does not now find so many supporters as it had when first promulgated by Darwin" (1909: 369).

A second, and for Warming more likely possibility, was that mutations were responsible for adaptation or epharmony. That mutations occur, Warming claimed, was an experimentally proven fact. However, although mutations may explain the presence in plants of useless or non-adaptive characters, Warming did not believe that mutations could account for epharmony; the vast majority of mutations will be maladaptive and disappear within a few generations.

For Warming the most likely hypothesis was that new forms arise in nature by the direct interaction of the environment on the plant body and the transmission of these alterations into the hereditary material of the plant. This was only a hypothesis and required more proof to become experimentally verified, but nonetheless Warming was still able to conclude that:

It seems beyond doubt that characters peculiar to growth forms have arisen through direct adaptation to the environment of natural self-regulation operating through countless generations, and that at the same time the acquired characters have been fixed to a greater or lesser extent by heredity (which is antagonistic to new adaptations). In this matter Lamarck had a keener eye for the truth than many investigators appear to suggest ... Direct adaptation is beyond doubt one of the most potent evolutionary factors in the organic world, and appears to play the leading role in the adaptation of growth-forms and formulations.

(Warming 1909: 373)

Schimper's work leaned heavily on Warming's, more so than he ever admitted (cf. Goodland: 1975). Like Warming, Schimper was a neo-Lamarckian. Changes in plant form due to purely hereditary factors might, he conceded, play a role in the acquisition of non-adaptive features, but the adaptive features of the plants form arise through the direct action of the environment (Schimper 1903: v).

By 1910 Warming's "infant science" of ecology was becoming a sturdy adolescent. As Lowe (1976) has documented, the period from 1900 to 1920 saw, in Britain, the emergence of ecology as a professional scientific discipline along the lines laid down in the nineteenth century for physics and chemistry. A key date in this

process was the founding in 1913 of the British Ecological Society. A.G. Tansley was the first president and the vice-presidents were W.G. Smith and F.W. Oliver. The society's Journal of Ecology also first published in 1913 and, from 1917 onwards, edited by Tansley has continued to be the major publication source for ecologists in Britain.

Experimental techniques and methods developed rapidly in ecology and Lowe (1976) has argued that this research strategy can be linked to the developing social relations between amateurs and professionals in British ecology throughout this period. The new professional ecologists such as Tansley and Oliver were in an ambiguous position regarding the strong amateur traditions of vegetation surveying and mapping which had been the centre of "ecological" concerns in Britain in the period prior to the emergence of ecology per se. On the one hand the army of amateurs in the local natural history societies were a resource which ought to be utilised; on the other, the new professionals were keen to demonstrate the need for a discipline of ecology which was not based in amateur natural history. The conflict is well brought out in R.L. Praeger's presidential address to the British Ecological Society in 1922:

... from the beginning of our field work the question why kept intruding itself, becoming more insistent and more clamorous as time went on ... So it came about that the glorious days of the primary survey, when we ranged free over moor and mountain, to a great extent were superseded. Our campaign took on a new phase, and weapons of greater accuracy were required. Six-inch map, binocular and pencil were replaced or at best reinforced by instruments for measuring the amount and variation of light, heat, moisture and by the whole battery of the chemical laboratory.

(Praeger, quoted in Lowe 1976: 529)

In their desire for experimental methods and rigorous techniques and theory many of the new ecologists saw a strong link between ecology and physiology. Isaac Bayley Balfour in the introduction to the English edition of Warming's textbook described ecology as the meeting ground of morphology, physiology and systematics, but the new ecologists were often critical of traditional taxonomic methods and practice. Lowe (1976: 522) claims that, "a widespread disillusionment with traditional systematics" was prevalent even in the 1880's. However,

the most vitriolic attack on traditional systematics was that launched by F.W. Oliver at a meeting of the British Association for the Advancement of Science in 1906. In the context of a general review of the state of botany in England, Oliver praised the physiological work being done by figures like Thiselton-Dyer and Vines but was scathing in his remarks concerning traditional systematics. Of herbaria he argued that "the effort involved in their upkeep is altogether disproportionate to any service to which they are put" (Oliver 1906: 735). He suggested a merger of the Kew and British Museum herbaria, and he ended his review by arguing that taxonomists must cease their concern with general floras and large scale monographs and concentrate on more detailed systematic, physiological and ecological studies of two or three species. Only in this way would they "contribute essentially to the science" (Oliver 1906: 737).

Similar developments were taking place in American ecology during this period. The Ecological Society of America was founded only two years after its British counterpart, in 1915, with its first president the zoological ecologist V.E. Shelford. By the end of its first year it had 307 members. McIntosh (1976: 353-356) has described the period in American biology from 1900 to 1920 as one which saw "the rise of a self conscious ecology." Amongst the major figures in American plant ecology during this period McIntosh lists J.M. Coulter and H.C. Cowles at Chicago, and C.E. Bessey and F.E. Clements at Nebraska. It was the last of these figures, F.E. Clements, who also founded the first American school of experimental systematics.

F.E. Clements, H.M. Hall and the First American School of Experimental Taxonomy

Frederick Edward Clements (1874-1945) was born in Lincoln, Nebraska and graduated with a B.Sc. from the University of Nebraska in 1894. An M.A. in 1896 was followed by a Ph.D. in 1898 on the phytogeography of Nebraska, both obtained while Clements was employed as an assistant of botany in the University. After the award of the Ph.D. Clements became associate professor of botany at Nebraska, a post he held for nine years. In 1906 he was appointed professor of plant physiology, but a year later he moved to the University of Minnesota as head of the department of botany, where he remained until

1917. The remainder of his academic life (1917-1941) was spent as a full-time research associate for the Carnegie Institute of Washington. Under the patronage of the Carnegie, Clements was able to set up an alpine laboratory at Pikes peak near Manitou Springs, Colorado, and in this way the Carnegie's resources were made available to doctoral students at Nebraska, which became "the top institution for studying grassland ecology" (Tobey 1977: 31). Although primarily concerned with pure science, Clements was also interested in applied aspects of plant ecology and especially with the application of ecological principles to the management of the American prairie grasslands. Clements was married in 1899, to one of his research students, Edith S. Clements. He died at Santa Barbara, California in 1945.³

Clements developed an early interest in cryptogams⁴ and, while a student at Nebraska he had studied under the great American mycologist C.E. Bessey. Several of his earliest published papers were concerned with the taxonomy of cryptogams (e.g. Clements 1897a, 1897b; Pound and Clements 1896) and this was a subject to which he devoted some attention even in his later life (e.g. Clements and Shear 1926, 1931). One of the most interesting of these early papers dealt with the classification of lichens (Clements 1897b). Lichens are a difficult group of plants to deal with taxonomically because they consist of a symbiotic association of two plants - an alga and a fungus. They are normally treated as a separate class of plants, even though in evolutionary terms lichens have almost certainly arisen more than once from different fungal stocks. Clements argued that the separate systematic treatment of lichens was wrong, that lichens were basically fungi, and that the two classes of "lichen" and "fungi" should be merged into a single class. The paper is worthy of note because it shows that, even at this early stage, Clements was committed to the idea that scientific classifications should be phylogenetic, i.e. that

3. These details of Clements' biography are taken from an obituary by Tansley (1946).

4. Cryptogams are plants which reproduce without seeds. They include algae, fungi, lichens, bryophytes (mosses and liverworts) and pteridophytes (ferns and their allies).

they should reflect evolutionary lines of descent.

However, it was in the newly developing field of ecology that Clements made his major mark on American botany. The ecological aspects of his research have been examined by a number of recent historians (e.g. Worster 1977: 205-220; Duff 1975) and will only be briefly treated here. According to Worster (1977: 209), "no individual had a more profound impact on the course of American as well as British ecological thought."

Clements' principal ecological concern was with plant succession and the dynamical aspects of successional change (cf. Clements 1905, 1916, 1929a, 1936; Clements and Weaver 1924; Clements and Shelford 1939). Natural communities of plants change and develop in an orderly way; as a lake becomes gradually silted up it will develop into a reed-marsh, then into scrub, then into birch and finally into an oak forest. Clements' research was concerned to locate the causes and dynamics of succession. Indeed, he called his new discipline "dynamic ecology". A major, although not novel, aspect of Clements' theories about succession was his belief that the final vegetation which develops in any locality (the climax) is determined solely by climate. A second vital aspect of his work was the claim that the climax vegetation is a "complex organism" and that it develops in a manner analogous to the development of the individual plant or animal. In the development of vegetation the individual plant and animal species are "coactors in a complex of effects proceeding from the habitat as the cause" (Clements and Shelford 1939: 21).

The methodological concerns of the new dynamic ecology were quantitative and experimental. The cause-and-effect relationship between plant and habitat represented the key to understanding vegetation and this relationship could only be studied by means of experiment:

It is not yet generally recognised that the term ecology connotes a study of the relation between organism and habitat, which demands the use of exact methods. For this reason it appears fortunate that the floristic study of vegetation, so much in vogue on the continent of Europe is rapidly coming to be known as plant sociology. To the ecologist, however, the cause-and-effect relation between plant and habitat is more than ever the central and vital part of botany, in the investigation of which quantitative methods alone can yield results of fundamental value.

(Clements and Goldsmith 1924: 3)

Clements' concern was that studies of vegetation should be experimental and his beliefs about the casual effects of habitat upon vegetation development were reflected in his writings on speciation and evolution. For Clements, like De Vries and Lotsy, the question of speciation was an experimental question. But, where for the geneticists it was experiments in the laboratory which would determine the nature of the process, for Clements it was a matter for ecological concern:

Experimental evolution will solve a taxonomic problem as yet untouched, namely the effect of recent environment upon the production of species ... Indeed the whole question of the ability or inability of environmental variation to produce constant species is one that must be referred to repeated and long-continued experiment in the field.

(Clements 1905: 13)

In some of his early writings on evolution Clements tried to abandon the term "species" altogether, which he felt had become "so vague that it no longer has definite meaning from the standpoint of evolution" (Clements 1907: 185). The chapter of his textbook Plant Physiology and Ecology (1907: 185-201) devoted to evolution is entitled "the origin of new forms" rather than the origin of species. In it Clements began his account with a discussion of Darwin's work. Following Darwin, he recognised the existence in nature of two types of variation: definite variations caused by the direct influence of environment on the plant and indefinite variations or variations due to chance. Darwin had held that new species arose through the action of natural selection on indefinite variation. Clements disagreed with this. Of the four possible mechanisms of speciation considered by Clements (the other three being mutation, hybridization and adaptation) natural selection is, "the only one not experimentally proven" (Clements 1907: 189). Darwin's failure to recognise this, Clements blamed partly upon the fact that Darwin founded his theory of evolution on observation rather than experiment.

Of mutation, Clements accepted that, "a careful examination of De Vries' results leaves no doubt that mutation is proved to be one of the methods by which new forms originate" (Clements 1907: 190). However, he denied that it followed from this that mutation is the major process by which new forms originate, as De Vries had maintained. A third

possibility is that new forms arise by hybridization. Of hybridization Clements (1907: 198) argued that it seemed to be a common mode of evolution in nature, although he went on to state that only a few cases have been examined where hybridization has been experimentally verified.

Clements claimed that it was by adaptation that most new forms arise in nature. A new form which had arisen in this manner Clements called an ecad. Whether such ecads were formed depends upon the plasticity of the parent species from which they evolve. A very plastic species will give rise to a new ecad wherever it migrates to a new habitat or its old habitat changes. An ecad placed back into its parents' habitat will revert to its parental type, although, if it has been in its new environment for a long period, this process of reversion may take years or even centuries:

In amount of difference they (ecads) are as distinct as many new species and have often been described as such. Whether they are species or not depends entirely upon the meaning given to this term.

(Clements 1907: 193-194)

Stability is merely stability of habitat. The longer a plant grows in a given habitat, the longer it carries on its functions and growth in a certain way, and the more difficult evolution of new forms becomes.

Thus for Clements the "forms", "varieties" and "species" of the traditional systematists disappear and are replaced by four terms, which relate the nature of a given plant form to its mode of origin:

1. There are new forms which arise by adaptation and which Clements termed ecads.

2. There are new forms which arise by the action of natural selection on indefinite variation; Clements termed these variants, although the existence of such variants is not an experimentally demonstrated fact.

3. There are new forms which arise by mutation, as in Oenothera lamarckiana; these Clements termed mutants.

4. There are new forms which arise by the hybridization of two previously existing forms; these Clements termed hybrids.

The four basic processes of evolution: adaptation, mutation, hybridization and (possibly) natural selection act more-or-less

independently to produce new forms. Isolation plays no role in adaptation or mutation and is a positive hindrance in hybridization. Mutants, hybrids and ecads probably often arise at more than one place and time, but migration makes this a difficult point to prove except by experiment. The origin of new forms, for Clements, was a complex issue and its study "must be left to the specialist" (Clements 1907: 201).

As he made clear in a later publication, Clements (1925: 309-312) conceived of adaptation or ecogenesis⁵ as a process which took place in two steps. The first of these, adaptation in the strict sense, is the production of new forms by change in the environment. The complement of adaptation is fixation. By fixation was meant, "the accumulation of a new habit or response until it becomes hereditary" (Clements 1925: 311; and see also Clements 1926: 335-339). Fixation does not account for the origin of new forms but it does account for their constancy or stability when transplanted. And fixation is only relative. No form will remain constant forever under the impact of a new environment (Clements 1929b: 378).

Clements' interests in taxonomy stemmed directly from this commitment to a neo-Lamarckian theory of evolution. He was aware of the transplant experiments which had been carried out by Bonnier in France and he began his own series of transplant experiments in order to test the results which Bonnier had obtained (cf. Clements 1929b: 357-259). However, an interest in the mode of origin of new "species" or forms was not the only reason that ecologists at the turn of the century had for castigating the treatment of species by traditional systematists. Another potent source of dissatisfaction were the disagreements going on within taxonomy between "lumpers" and "splitters". Before looking at Clements' taxonomical work it will be necessary to deal briefly with this issue.

The differences between lumpers and splitters had its origins in the work of Jordan discussed in Chapter 3. Jordan had shown that many so-called "varieties" within the Linnaean species bred true under cultivation, and by the turn of the century this fact was well known to

5. In his later writings Clements often gave preference to this second term. It is derived from Latin, meaning literally genesis by the environment or "ece-".

taxonomists. Some systematists, following Jordan's lead, began to give species names to all forms previously regarded as having only varietal or sub-specific taxonomic status. These were the "splitters". "Lumpers", on the other hand, kept to the broad species concept of Linnaeus and gave units within the species only varietal recognition, regardless of whether the forms so described would probably breed true if grown in cultivation.

The attractions of species-splitting to the taxonomists were obvious. Within the taxonomic community prestige was and still is attached to the naming of new species. Species-splitters did not have to travel to exotic new lands in order to find new species to name and describe: they could find hundreds of new species even in well-known floras. However, ecologists like Clements were incensed at the use of Latin binomials in this fashion, because it made the task of vegetation analysis and description almost impossible:

... there can be no real taxonomy as long as the sole criterion of a species is the difference which any observer thinks he sees between one plant and another. The so-called species of today range in value from mere variations to true species which are groups of great constancy and definiteness. The reasons for this are obvious when one recalls that 'species' are still the product of the herbarium, not of the field, and that the more intensive the study, the greater the output of 'species' ... The existing practice of re-splitting hairs must come to an end sooner or later. The remedy will come from without through the application of experimental methods in the hands of the ecologist and the cataloguing of slight and unrelated differences will yield an ordered taxonomy.

(Clements 1905: 12)

The passion which could be aroused on this subject is shown by the meeting in Chicago in 1908 of the Botanical Society of America on "aspects of the species problem." Bessey, Cowles and Clements were all invited to attend and all three used the occasion to deliver attacks on traditional systematics. The substance of Bessey's (1908: 218-224) argument was that species are conventional collections of individuals and that, therefore, they should be made with practical ends in mind. He complained bitterly that "much of the species-making in recent years has rendered it vastly more difficult than formerly for us to grasp the flora of a region ... We are in danger of destroying the usefulness of taxonomy in our zeal for describing

every differing form as a separate species" (Bessey 1908: 219). Taxonomists, he concluded, needed reminding that taxonomy was not just for them but for all botanists.

Cowles agreed. What a species was still required experimental and ecological investigation, but he was sure that "one of the noblest aims of ecology is the destruction of many of the 'species' of our manuals" (Cowles 1908: 266). Cowles concluded his polemic with the dire warning that:

The recent ebullitions of the taxonomic radicals have evoked in botanists in general successively, dissatisfaction, contempt and rage. These things will not be endured much longer; a little more and the sinning taxonomist will be cast into the outer depths where there will be much wailing and gnashing of teeth.

(Cowles 1908: 271)

Clements (1908) also produced an account which was highly critical of orthodox taxonomy, but unlike his counterparts, he suggested a nomenclatural solution to the problem of the new "varietal species". This is that these "species" should be given, not binomial, but trinomial names. And the form of the trinomial used should be a reflection of the putative mode of origin of the form being described. Thus for an ecad the third name used should reflect the habitat factor which led to the ecad's production, e.g. scias in the case of a shade form. For mutants the trinomial should have attached to it the prefix per. For postulated variants (Clements repeated his claim that this is not an experimentally verified mode of evolution) any prefix may be used provided it does not conflict with the trinomials used for ecads. For hybrids the already established X-nomenclature could be used.⁶ In this way, the new "species" of the herbarium taxonomist disappear and are replaced by categories which tell the mode of origin of the form concerned. Clements (1908: 264) ended his paper by giving four examples of "species" which he intended to "sink" in this manner:

1. Cerastium oriophilum = Cerastium strictum scias (ECAD: shade form of C. strictum).

6. Using this nomenclature a hybrid is named from its to parental species together with an X to signify that hybridization has taken place.

2. Aquilegia jamesis = A. coerula peralba (MUTANT: mutation from the parental species, A. coerula).
3. Verbena intermedia = V. stricta x hastata (HYBRID: the parental species being V. stricta and V. hastata).
4. Machaerathera aspera = M. viscosa aspera (M. viscosa aspera was believed to be a VARIANT of the parental form, M. viscosa).

The ecad, mutant, hybrid and variant are experimental categories. To use them field and laboratory methods are required; herbarium studies alone are inadequate. The experiments on which these categories were based were transplant experiments. Clements had begun this research in 1901, after reading Bonnier's work, but the experiments were interrupted by his move to Minnesota and not resumed until 1917 when he joined the Carnegie. In the period after 1917, these experiments were organised not by Clements alone but in conjunction with the taxonomist and phytogeographer H.M. Hall.

Harvey Monroe Hall (1874-1932) was a graduate of the University of California at Berkeley where he was a student from 1898 to 1901. Hall's original interests in biology stemmed from a concern with natural history and his earliest publications were on the life-history and behavioural habits of birds. His M.Sc. at Berkeley (Hall 1902) was a phytogeographical survey of the San Jacinto mountains in Southern California. After its completion Hall remained at Berkeley and in 1906, completed his doctoral research on the systematics of the Compositae, a group in which Hall maintained an active taxonomic interest throughout his research career. During this period Hall was in charge of the University Herbarium at Berkeley and later (after 1903) an instructor of botany in charge of the botanic garden. In 1908 he was appointed assistant professor and in 1916 associate professor, a post that he held until joining the Carnegie in 1919. He remained with the Carnegie for 13 years, this being the period of his active research in experimental plant taxonomy. He died suddenly in 1932 at a period when his work was just beginning to receive its greatest recognition.⁷

Even in the early years Hall's taxonomic research employed a very

7. These biographical details of Hall's life are taken from an obituary by Babcock (1934).

broad species concept; Hall was a "lumper" and not a "splitter". His Ph.D. thesis described only three new species, an unusually low number for a taxonomic monograph in this period (cf. J.M. Coulter's 1908 review of the published version of the thesis). Hall was not against the recognition of intraspecific variation, but he argued that such forms should not be given binomial names:

The systematist who is more concerned with problems of genetics than he is with the naming of new forms will ultimately be able, as the result of extended field observations and cultural experiments, to reduce these "species" properly to subordinate rank, indicating their relationship by the ordinary methods.

(Hall 1912: 195)

Hall's close association with Clements began with his move to the Carnegie in 1919 and for the next three years they were active co-workers at the Pikes Peak alpine laboratory in the Colorado Rocky Mountains. The result of their joint labours was the publication in 1923 of The Phylogenetic Method in Taxonomy, a work which represented the first attempt to construct an experimental taxonomy and apply it to a substantial portion of the flora of a particular geographical region.⁸

The central theme of the Phylogenetic Method was that all classifications of plants should reflect evolutionary relationship, i.e. phylogenetic lines of descent. To demonstrate these relationships phylogenetic charts were constructed for all of the groups studied (an example of one of these charts is shown in figure 4.1). The authors were extremely critical of orthodox, herbarium taxonomy which, in their opinion, failed to arrive at classifications which were phylogenetic and not artificial:

... the mere recognition of supposed new species in the herbarium hardly merits the term descriptive botany and it can in no wise be regarded as adequate taxonomic investigation. It has its value, and hence its excuse, in the biological exploration of new and distant countries, but, here as elsewhere, permanent taxonomic results must await the application of statistical and experimental methods in the field.

(Hall and Clements 1923: 1)

The experimental methods used were of five kinds:⁹

8. In the text which follows this work is referred to by the abbreviated title of "Phylogenetic Method".

9. The methods used by Clements and Hall in their experimental taxonomy are described both in the Phylogenetic Method (pp. 19-23) and elsewhere (Clements 1928: 292-293; Hall 1929a).

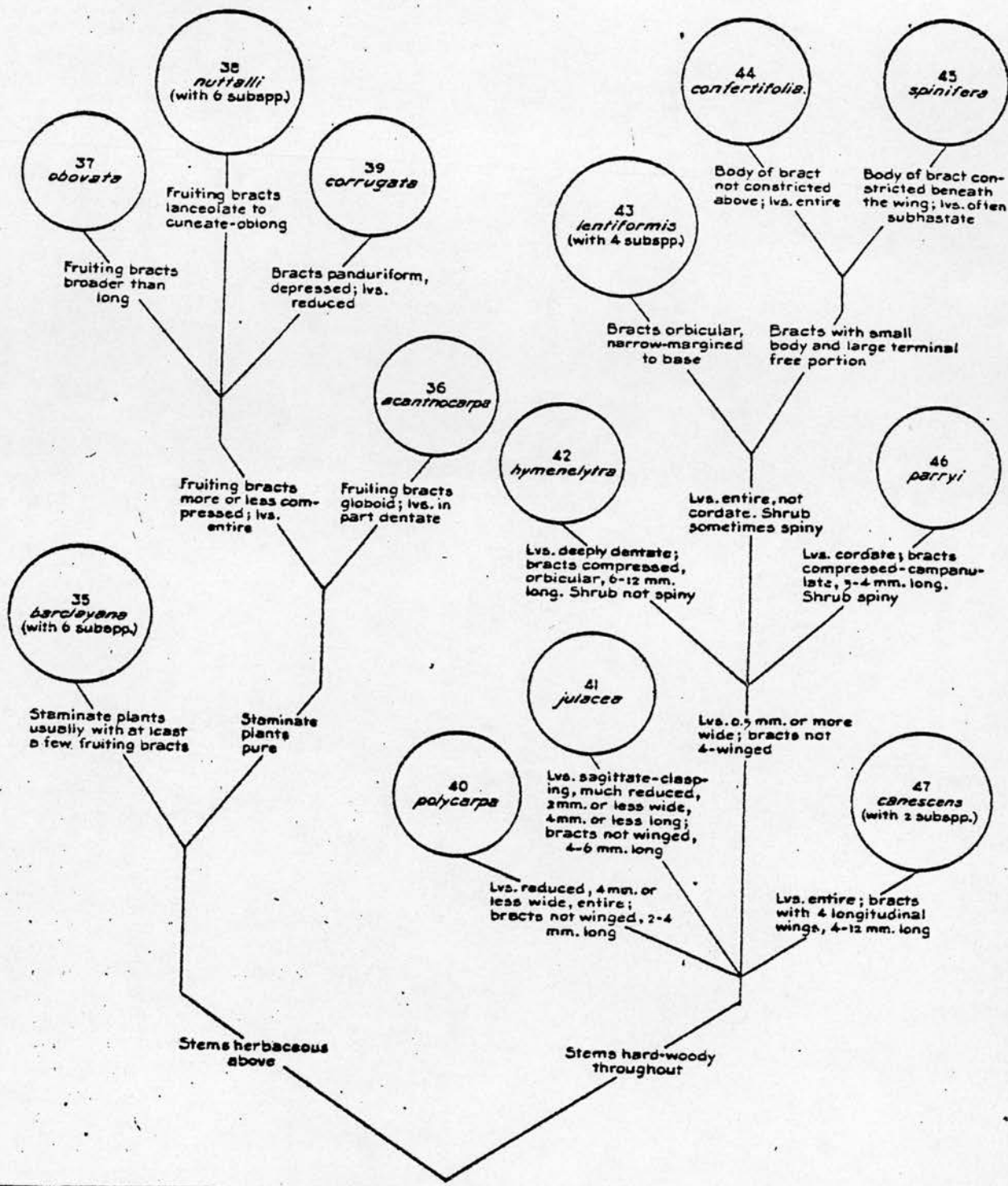


Figure 4.1. A Phylogenetic Chart of part
of the genus Atriplex (from Hall and
Clements 1923:314)

1. The transplanting of similar but unlike forms of perennial species into a uniform environment. This was the most obvious method for testing the effects of habitat on plant growth and had been the method adopted by Jordan and by Clements in his earlier work.

2. The growth of seedlings of related annual forms under uniform conditions.

3. The transplanting of a single perennial form into diverse environments. (This was the varied-environment method of transplanting which had been used by Bonnier and again by Clements in his earlier research.)

4. Reciprocal transplanting, which was a method devised to deal with cases where two closely related forms or species occupied similar habitats. Plants of each type were transferred, not just to the other habitat but to the actual hole left by the removal of the first plant. The object of this method was to ensure exact reversal of conditions and thus ensure a clear-cut demonstration of the extent to which different species of plants can be changed from one kind to another.

5. Habitat inversion, that is, the altering of the environment around a plant in order to assess the effect on its growth (e.g. the removal of shade cover in order to study the effect of direct sunlight upon the plant's growth).

Concerning the evolutionary implications of their research the authors repeated the claim made by Clements two decades earlier, that adaptation is the key evolutionary process:

Further studies of origin at the Alpine Laboratory have confirmed the hypothesis that direct adaptation to the habitat has there produced the largest number of new forms of plastic species. Mutation now seems less important than it did 15 years ago, but this is partly due to the increasing difficulty of distinguishing mutants from variants, and sometimes even from ecads. Much variation is undoubtedly a response to the gradual change of an efficient factor, or to minute habitats of varying intensity. Further search has not increased the small number of probable hybrids; and it has become necessary to attempt the direct production of hybrids in nature. In spite of the changing importance of the methods of origin, it still appears certain that adaptation, mutation, variation and hybridization comprise four basic processes of evolution, though it now seems evident that adaptation and hybridization constitute the two basic modes.

(Hall and Clements 1923: 23)¹⁰

10. This passage is noteworthy because in it Clements does seem to allow that natural selection can play a role in speciation. However Clements is inconsistent on this point and in later works he returned to his original position viz. that there existed no experimental proof for the origin of new forms by selection.

In their taxonomic treatment of the plants on which these experiments had been conducted Hall and Clements employed a very broad species concept. This was in agreement with their own views concerning the use of binomials but at variance with recent trends in floras of the Rocky Mountain vegetation.¹¹ Species-splitting was severely criticised: "it is imperative to establish species on the basis of the theoretical concepts as exemplified by Gray and those who have worked in a similar manner since" (Hall and Clements 1923: 15).¹²

Intraspecific categories are recognised but given trinomial names. Where possible these trinomial forms were referred to by their means of origin, i.e. as "ecads", "mutants", "variants" etc. Where the mode of origin is unknown or unclear the neutral term "variad" was employed (Hall and Clements 1923: 23). The underlying purpose of this scheme of nomenclature was to create, in effect, two systems of classification: the first was a series of broadly-conceived species of value to the amateur botanist and floristic ecologist; the second was a series of minor forms or variads of value to the specialist in genetics, experimental ecology and evolutionary theory. However, as the authors made clear, both these "systems" must be based primarily upon evolutionary relationship rather than convenience. As for the species itself, this was defined as "a definite phylogenetic stock, sprung from and related to similar stocks, and itself undergoing modification into a number of variads" (Hall and Clements 1923: 11).

In the Phylogenetic Method Hall and Clements were only able to apply their experimental taxonomy to three genera of the Rocky Mountain flora - Artemisia, Chrysothamhus and Atriplex. These groups were chosen partly because they had many species undergoing active evolution and partly because many of their species have medical, agricultural or horticultural importance. However, in their introduction the authors promised that more monographs, dealing with all the major genera of North America would eventually be prepared.

-
11. The most notable difference is with Rydbergs (1917) flora. Rydberg had described 5,100 species. In Clements flora (Clements and Clements 1914) the same geographical area is covered but only 1,878 species are considered to be present.
 12. The reference here is to the great nineteenth century American taxonomist Asa Gray, who was noted for his use of a broad species concept.

A direct opportunity to assess the impact of the new experimental taxonomy presented itself at the International Congress of Botanical Science held at Ithaca, New York in August 1926. Hall presented two papers to the congress (Hall 1929a, 1929b), the first dealing with the taxonomic treatment of intraspecific variation and the second with the natural basis of taxonomic categories. Both papers stressed the need for experimental methods in taxonomy and the necessity of synthesising traditional taxonomic methods with the new fields of cytology, genetics and ecology. The second of these two papers particularly emphasised the importance of genetics and cytology and was delivered before a joint session of the sections of the Congress dealing with taxonomy, cytology and genetics. Many prominent geneticists and cytologists were at the meeting including Otto Heilbron, Bradley M. Davis and George S. Shull.¹³ The taxonomists present included Karl M. Wiegand and Paul Rydberg (see table 4.1).

Hall's paper received a generally enthusiastic response from the geneticists and cytologists. However, the taxonomists present were sceptical. Wiegand (1929b), in his reply to Hall's paper, made an argument which was to become standard in later clashes between experimental and orthodox systematists. He admitted the value of experimental methods, but he denied their general applicability to taxonomy on grounds of practicality:

With regard to the question of experimental taxonomy I stand ... in the belief that while data obtained in this way are very desirable and are often capable of throwing great light on the significance of morphological differences, they are not usually of practical value to the general taxonomist. Such data are often impossible to obtain, sometimes because of the unavailability of the living material, sometimes because, as in the case of woody species, the time required to grow the plants is too great, but often also because of the large number of plants concerned.

(Wiegand 1929b: 1575)

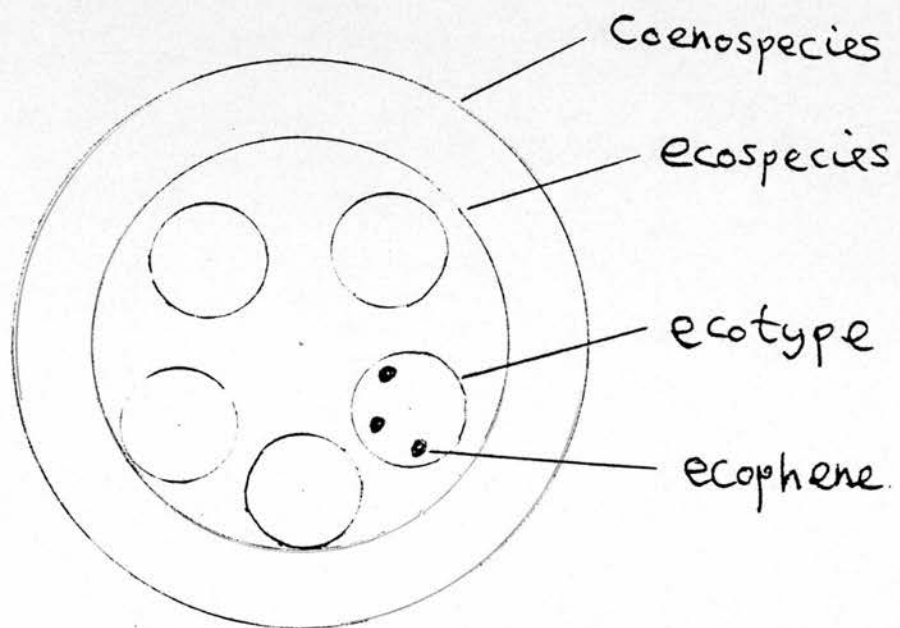
However, the most vitriolic attack on Hall and Clements' work was made by Rydberg, a taxonomist at the New York Botanical Garden. He had special reason to dislike their work, because his own Rocky Mountain flora (Rydberg 1917) had been severely criticised in the Phylogenetic Method and many of the new species which he had described for the area had been treated by Hall and Clements as variants. His paper to the

13. The work of Bradley M. Davis on Oenothera was discussed briefly in Chapter 3. Otto Heilbron was a Swedish cytologist and George Shull a geneticist whose work was later cited by Clausen's group.

Table 4.1. Speakers at the discussion on
"Taxonomic Units and their Natural Basis"
held at the International Congress of
Plant Science, Ithaca, New York, Aug. 20. 1926.

H. M. Hall	Experimental Taxonomist	Carnegie Institution
K. M. Wiegand	Taxonomist	Cornell University
P. S. Rydberg	Taxonomist	New York Bot. Garden
R. A. Harper	Taxonomist	Columbia University
O. Heilbron	Cytologist	Stockholms Högskola
W. R. Taylor	Cytologist	U. of Pennsylvania
G. S. Shull	Geneticist	U. of Princeton
B. M. Davis	Geneticist	U. of Michigan

Figure 4.2. Genecological units (from
Turesson 1922b : 344)



conference (Rydberg 1929) took the form of a critical review of the Phylogenetic Method. These criticisms fell into three categories. He objected to the broad species concept employed by Hall and Clements and the consequent use of trinomials. He objected to the use of experimental methods, which he argued had been of less importance to Hall and Clements' methodology than they themselves had made out. And, he objected to the tone in which the criticisms of traditional taxonomy had been made:

The objections (of ecologists about taxonomy) might have been warranted but they should not have been presented in an overbearing and sarcastic way. I felt strongly tempted to give them some of their own medicine. How can ecologists teach taxonomists the way to do their work?

(Rydberg 1929: 1540)

Rydberg defended a narrow species concept based on morphological criteria by a kind of Baconian inductivism: "until the flora of a country is perfectly known all forms existing should be described ... I leave it to others to find out whether the characters, prominent or trifling as they may seem to be, ... are constant enough to place them as distinct species" (Rydberg 1929: 1544).

As several other papers delivered to the conference show, this was not a position with which many taxonomists were in agreement. They were too well aware of the disrepute which was following in the wake of species-splitting (cf. Wiegand 1929a; Skottsberg 1929). However, they did not see the return to a broad species concept as entailing, of necessity, the use of experimental methods.

In the years which followed the publication of the Phylogenetic Method the links between the research of Clements and Hall became more tenuous. From 1922 onwards Hall, although still on the staff of the Carnegie Institute, returned to California to resume his studies of the flora of the Sierra Nevada mountains. The original objectives of this research were to repeat the same kind of transplant experiments already being done by Clements in Colorado (cf. Clausen, Keck and Hiesey 1940: 4). Although this work was initially under Clements' direction, in later reports to the Carnegie Institute it was given a separate account, within the general division for plant biology.¹⁴

¹⁴. This change takes place in Carnegie Institution year books published after 1927.

Hall never lost contact with the Californian biologists and especially with E.B. Babcock. A paper written with Babcock (Babcock and Hall 1924) shows that the two authors were aware of the work of T.H. Morgan and his associates on the genetics of Drosophila. Of special interest in this paper is the authors support for Morgan's claim that mutation and natural selection are the major processes of evolution and that these two processes act not separately but in conjunction. A neo-Lamarckian mode of speciation is not ruled out because concerning mutation itself the authors note that, "the cause of these changes is not known ... the environment may have something to do with it" (Babcock and Hall 1924: 81). However, Heiser calls this paper, with its emphasis on the study of chromosome numbers and artificial hybridization, "One of the first truly biosystematic papers to emerge in the United States" (Heiser 1969: 111).

Towards the end of his life Hall clearly became dissatisfied with Clements' theories concerning adaptation and ecogenesis. In their report to the Carnegie Institute in 1927 Hall and his co-workers (Hall, Keck and Hiesey 1927: 312) suggested that their results were compatible either with the view that environment was selecting biotypes or with the theory that ecological factors act directly to bring about changes in the plants' growth. A similar position was adopted by Hall in the discussion of speciation in his 1928 monograph on Haplopappus:

Whether or not a somatic modification may in time effect the germinal constitution, and also the role of environment in direct induction of genetic change, are problems of fundamental biological significance; but they are not primarily taxonomic ... Such discovery must await attack by combined analytic and synthetic methods of research on the respective roles in evolution played by mutation, hybridization, somatic modification, isolation and natural selection.

(Hall 1928: 7-8)

Although he lived 13 years longer than Hall, Clements never adjusted his views on speciation to what, by the late thirties and early forties, had become the prevailing orthodoxy in evolutionary biology. In his final book, Adaptation and Origin in the Plant World, which was not published until 5 years after his death. Clements repeated the claims of his earlier research, viz. that adaptation is the major mechanism of evolution and that there is no direct experimental evidence to verify Darwin's theory of evolution through natural selection:

Adaptation is a universal process, brought about by response to direct physical factors and expressed both in function and in form. For all the species employed, there is no evidence that it arises through the selection of genetic strains or variations ... Natural selection does not operate upon the forms produced by adaptation, since they are immediately in harmony with the environment that produces them.

(Clements, Martin and Long 1950: 260-261)

In this work there is little discussion of Clements' neo-Darwinian opponents. In a brief mention of Turesson's transplant experiments, Clements acknowledged that many of his ecads had been described as ecotypes by Turesson and found to be fixed and stable genetical strains. Commenting on this the authors add that "it is possible, though hardly likely, that they are of different character on the two continents, and the more probable explanation is that they are neither completely fixed, nor wholly unstable" (Clements, Martin and Long 1950: 257). The treatment of Clausen's work was even more perfunctory; the authors simply note that "a thorough exploration of the part that genetics play in the nature of species has been made by Clausen, Keck and Hiesey" (Clements, Martin and Long 1950: 170).

Although Clements' evolutionary views were later discredited and the work of Hall and Clements ignored by later generations of bio-systematists, their research presents the first major attempt to introduce experimental methods into taxonomy. The objectives of their research were two-fold: to discover the mode of speciation in plants and to use that knowledge to produce an experimental classification along evolutionary lines. These twin aims: to study evolution at work and to construct a taxonomy based on that study, were to remain the central objectives of most experimental taxonomists until after 1950.

Leonary Cockayne and Experimental Ecology in New Zealand

America was not the only country where an experimental taxonomy founded upon ecology was being advocated in the period from 1910 to 1930. A similar goal was evident in the work of the New Zealand ecologist Leonard Cockayne (1855-1934).

Cockayne was British by birth and had originally trained in medicine but moved, for health reasons, to Australia in 1879 and then to New

Zealand in 1881. An amateur and of independent means he has, nevertheless, been described as New Zealand's "greatest botanist" (Laing 1936: 457).¹⁵

From his very earliest papers Cockayne's major interest in botany was in the ecological study of vegetation and its relation to the problems of evolution. Cockayne was aware of the mutation theory of De Vries and he applauded its experimental approach to speciation (Cockayne 1912: 5). However, although he accepted that mutations sometimes occur, it was adaptation that he considered the major source of the variation upon which speciation could act:

It is when we come to epharmonic adaptations that ecology presents its most important contribution to the evolutionary question ... I am of the opinion that in the hereditary epharmonic variations cited below there is much greater likelihood of their having been brought about by the direct action of various ecological factors than by the continuous accumulative selection of fluctuating varieties.

(Cockayne 1912: 13)

Cockayne never rejected this position, but in his later writings (Cockayne 1923; Cockayne and Allan 1927b) he increasingly stressed the evolutionary importance of hybridization. He had read Lotsy's Theory of Evolution by Means of Hybridization and believed that it could not be "lightly dismissed" (Cockayne 1923: 105). In addition, he held that traditional taxonomists had underrated the significance of hybrids. To distinguish a hybrid morphological examination alone was not sufficient; the alleged hybrid's geographical locality should be traced and related to the geographical and ecological location of its parental species. Also, where possible, the alleged hybrid's offspring should be grown and studied, for these, if they were genuine hybrids, will be polymorphic (Cockayne 1923: 107). Both the stress on the importance of hybridization and the very critical approach to orthodox taxonomy are evident in the 1927 paper titled "The Bearing of Ecological Studies in New Zealand on Botanical Taxonomic conceptions and Procedures" (Cockayne and Allan 1927a). Although Cockayne and Allan, unlike Hall and Clements, did not make a significant contribution to the development

15. This article by Laing is an obituary. For another obituary of Cockayne see Allan (1935) and for a more recent assessment of Cockayne's work see Moore (1967).

of experimental taxonomy, their work clearly shows the faith with which the new 'dynamic' ecologists approached the old problems of plant classification. Beginning their article with some praise for those, including Hooker, who had preceeded them in their study of the New Zealand flora, the authors added that:

Without doubt, the accumulated results of their devoted labours represent all that could possibly be done by the herbarium method. But to recognise our indebtedness is not to deny that future work must proceed on other lines that lead to much more exact knowledge of the facts as they present themselves in the field and in the experimental garden.

(Cockayne and Allan 1927a: 235)

And the authors were highly critical of herbarium taxonomy, representing it as "mere guesswork" based upon grossly insufficient material supported by "scrap^pily and casually prepared notes" (p. 235). They ar^kgued that, in New Zealand at least, progress in classification had been made by ecologists rather than taxonomists. The reason for this was seen as being the taxonomists' adherence to the methods and techniques of the herbarium, or, as the authors themselves put it, "the herbarium or artificial method". The latter is a method which has "served its day and outlived its usefulness" (Cockayne and Allan 1927a: 250). Progress in taxonomy would only be made by new workers who were "free from the thralldom of the dangerous herbarium artificial method" (pp. 275-276).

The alternative to this methodology was the development of a "natural" or "field" taxonomy. The object of field taxonomy was to classify plants in the light of the new knowledge gained by ecological research. Its methods were those of field study, herbarium collecting and experimental studies under cultivation (Cockayne and Allan 1927a: 251-257). The value of such methods was that they "will prove of service to those collectors who have passed the stage of looking for 'new' species, or ransacking herbaria for scraps of 'puzzling plants' and who desire to do really useful work" (Cockayne and Allan 1927a: 251).

The terminology which Cockayne and Allan used in their work was derived mainly from the writings of Lotsy. Thus the basic working unit of field taxonomy was the jordanon and the major feature of such

groups is that they will breed true under cultivation. The simplest type of species found in nature are those composed of a single jordanon, these are simple species in Cockayne and Allan's terminology. More complex is the case where a group of jordanons occur "so closely allied that to treat them as a separate species would too much obscure this closeness of relationship." (p. 248). These are compound species, and within such taxa the individual jordanons should receive separate nomenclatural recognition as varieties. Where, as is frequently the case, jordanons have crossed to produce a very polymorphic species consisting of jordanons and hybrids, these species are Linneons in Cockayne and Allan's use of that term. Finally, in all these groups there may be epharmones, i.e. forms displaying variation due to environmental influences which are unstable and which will revert back to the "normal" mode of growth when planted in a different environment. The authors profess agnosticism about whether such variation can become inherited:

The taxonomist is not required to analyse in detail the various factors which by their combination produce the "epharmone" ... Into the vexed question whether an epharmone ever becomes so fixed as to result in the formation of a jordanon (heredity of an acquired character), we need not enter here. It is sufficient for the taxonomist and descriptive ecologist to know the status of his forms as they exist at the present time.

(Cockayne and Allan 1927a: 249)

To distinguish between jordanons, hybrids and epharmones requires ecological and genetic methods; for the herbarium taxonomist they are all entities of the same status, viz. "varieties" within the artificial species of the herbarium (Cockayne and Allan 1927a: 244).

This terminology, like the mutant-variant-hybrid-ecad system of Hall and Clements, was little used by later biosystematists. In part this was probably due to the reaction against Lotsy's views on evolution and speciation which took place in experimental taxonomy after the rise of neo-Darwinism in the 1930's and 40's. However, the major reason for its failure was the prominence by the 1930's of a rival system of nomenclature for experimental taxonomy - the genecological system formulated by the Swedish botanist Göte Turesson.

Göte Turesson and the Beginnings of Genecology

The ecologists we have dealt with so far had little detailed knowledge of plant cytology and genetics. Cockayne "took little interest in the minute microscope investigations of recent geneticists" (Laing 1936: 463). And, similarly, Clements "never seemed to give proper weight to the results of modern genetical research" (Tansley 1946: 196). However, a synthesis of the ecological and genetical approaches to the species problem is found in the work of the great Swedish pioneer of genecology, Göte Turesson (1892-1971).

Turesson was born at Malmö in Southern Sweden and completed a secondary education at Malmö and Lund before leaving to study in the United States in 1912. Turesson spent three years in America where he obtained a B.Sc. (1914) and an M.Sc. (1915) at the University of Washington in Seattle. Turesson's early botanical interests were in ecology and mycology, and the papers written during this period reflect this dual involvement; two deal with ecological themes (Turesson 1914, 1916a), and two are on mycology (Turesson 1915, 1916b). The last of these includes the description of a new species of Penicillium. His final year in America was spent working as a laboratory assistant to J.W. Hotson, a mycologist at the University of Washington.

When Turesson returned to Sweden he was, for three years, an assistant teacher in botany at the University of Lund. However, in 1918 he moved to the genetics department where he became a student of Herman Nilsson-Ehle.¹⁶ Nilsson-Ehle had been one of the first experimentalists to attempt to synthesise Mendelian genetics with Darwin's views on natural selection and had applied both perspectives in his own work on the genetics of breeding of cereal crops. He was also one of the earliest scientists to stress the enormous importance of recombination as a source of variation in sexually outbreeding species. Turesson's early papers owed a great deal to Nilsson-Ehle's influences, as he himself acknowledged (Turesson 1922b: 213). It was during his period in Nilsson-Ehle's department that Turesson obtained a B.Phil. (1920), M.Phil. (1921) and finally a Ph.D. (submitted in 1922, awarded in 1923). His doctoral thesis, "The Genotypical Response of the Plant Species to

16. The importance of Nilsson-Ehle's work has already been mentioned in Chapter 3.

Habitat", was concerned with the ecotype concept and was part of a series of papers on the nature of ecological variation within species, a subject that was to concern Turesson for the whole of his working life. The post at the genetics department was followed by a brief period as an assistant teacher of plant physiology and then by a post as a reader in botany at Lund, a position which Turesson held for 12 years until 1935. It was at this time that the most famous of his papers on genecology and experimental taxonomy were written. In addition to his association with the University of Lund, Turesson was also a director of the Weibullsholm plant breeding station at Landskrona (1928-1931). Turesson left Lund to take up a professorship of systematic botany and genetics at the Agricultural College in Uppsala, a post he retained until his retirement in 1959. He died in 1971, at the age of 81.¹⁷

The work which led Turesson to the discovery of ecological races within the Linnaean species, and thus to an involvement with experimental taxonomy, was concerned with the study of the causes of plagiotropy in maritime, shore plants (Turesson 1971, 1919). Plagiotropy is the tendency for some plants to take on a prostrate or horizontal growth form when grown in certain environments. Plagiotropy had been observed by other ecologists and was known to be especially common amongst plants growing on sand-dunes or near the coast. Turesson, then working for the summer at the ecological station at Hallands on the Island of Väderö, undertook some laboratory experiments to determine the cause of this growth habit. Warming (1909: 26-27) had argued that the probable cause of plagiotropy was the difference in temperature of the air and soil at the time when the shoots were developing, i.e. that it results from the execution of thermotropic movements by the plant. However, by growing plants in laboratory-controlled conditions, Turesson was able to show that the plagiotropic growth habit was a response to high light intensity and was thus a phototropic movement on the part of the plant (Turesson 1919: 13-24).

This early research exhibits the combination of field and laboratory analysis which were the hallmark of Turesson's later work.

17. These details of Turesson's biography were taken from an obituary by Müntzing (1971).

Also, and more importantly, Turesson made clear his own beliefs concerning the relationship between environmental and hereditary variations and between hereditary characters and habitat response. Thus, according to Turesson, plagiotropic plants are of two different kinds, viz. "modificatory prostrate forms, and hereditary prostrate forms" (Turesson 1919: 27). Both forms are sometimes found within the same systematic species. For example, Atriplex latifolium is usually an erect plant but will take on a prostrate growth habit under conditions of high light intensity. However, Turesson discovered a form of this plant, which he called A. latifolium prostratum, which was always prostrate in its growth habit regardless of light intensity. When Turesson planted this prostrate form in his own garden at Malmo it retained its prostrate growth habit through several generations, in spite of conditions of low light intensity. Turesson took this to be a proof of the hereditary nature of the growth response in this plant and was able to conclude that there exist in Atriplex "physiologically and genetically widely different races within the 'species' of the genus" (Turesson 1919: 29).

Many of these dominant themes concerning the nature of plagiotropy are manifest in the papers in which Turesson (1922a, 1922b) formally introduced the ecotype concept. A major aim of both these papers was to develop a method whereby environmental responses could be distinguished from hereditary variation:

An attempt has been made to show to what extent the behaviour of plant species in different habitats is the result of a direct response to the environment on the part of the individual plant, and to what extent it is due to the presence in the different habitats of different hereditary variation. While in some cases the observed characteristics were found to be purely modificatory, the differentiation of the species-population into different hereditary variations was found to be the rule in the majority of cases.

(Turesson 1922b: 331)

The method which Turesson used to distinguish between these two sorts of variation was transplantation into a uniform environment, i.e. the same method which had been used by Jordan. If the ecological varieties maintained their characteristic features and appearance over several generations, Turesson took this as proof, not that they were different species, but that they were fixed hereditary varieties within

the species. Varieties of this kind Turesson termed ecotypes. If, on the other hand, the ecological variety lost its special characteristics when grown in an experimental garden, then this was taken as proof that the variety arose in the wild through the action of the environment on the phenotype only. These varieties Turesson termed ecophenes. The transplant experiments on which this research was conducted were initially carried out in Turesson's own garden at Malmo. Later, when the number of transplants became too large for this, Turesson set up a permanent "ecotype garden" in the grounds of the Institute of Genetics in Akarp.¹⁸

The larger of the two 1922 papers (Turesson 1922b) presents the results of such transplant studies on 17 species in 13 widely distributed genera of flowering plants. Amongst the hereditary races discovered were shade forms of Lysimachia Vulgaris and Dactylis glomerata; coastal dwarf forms of Succisa pratensis and Centaurea jacea; and coastal succulents in Solanum dulcamara, Matricaria indora, Leontodon autumnalis and Melandricum rubrum. In one of the most closely studied species, Hieracium umbellatum, no less than five ecotypes were demarcated. All these ecotypes were distinguishable on the basis of external morphology, although the differences between them usually concerned features such as length of stem or leaves etc., which could only be expressed as mean differences between two populations rather than as discrete morphological markers. However, external characters were not the only means of distinguishing ecotypes; many were found to differ from each other in leaf and stem anatomy as well. Some of the ecotypes Turesson described had received prior taxonomic recognition as subspecies or varieties, but the majority had no official taxonomic status.

The ecotype was itself only one unit in a hierarchy of categories (see figure 4.2). For Turesson, "the species problem is ... in a large measure an ecological problem" (1922b: 344). New species arise as the "complicated products of recombined Mendelian factors, or genotype compounds" (Turesson 1922b: 342). However, the cause of such

18. In his attempts to get money for this venture Turesson enlisted the help of some powerful biologists. Amongst those who sent letters of support were J.B.S. Haldane and Nilsson-Ehle.

changes is selection in response to changes in the habitat:

A change in the non-living world brings about a corresponding change in the living, inducing a recombination of Mendelian factors now distributed in organisms, and resulting in the formation of new genotype compounds or species (= evolution).

(Turesson 1922b: 343)

In place of the traditional units of systematics (species and varieties) we get a system of classification which reflects this process of evolution through selection of inherited variation. The levels of this hierarchy were originally defined as follows:

Coenospecies: "The total sum of possible combinations in a genotype compound"

Ecospecies: "The Linnaean species or genotype compounds as they are realised in nature"

Ecotypes: "The product arising as a result of the genotypical response of an ecospecies to a particular habitat"

Ecophenes: "The reaction-types of the ecotypes called forth by the modificatory influences of extreme habitat factors"

(Turesson 1922b: 344-346)

Ecophenes possess the same hereditary constitution (genotype), even though they are morphologically distinct, and thus correspond to Johannsen's "phenotypes" (cf. Turesson 1922a: 111). Selection operates at the level of genotypical differentiation (i.e. on ecotypes). It does not operate at the level of the ecophene because variation of this type is not inherited. Adaptation takes place through the action of selection; it is not a phenomenon sui generis as had been claimed by the neo-Lamarckians (Turesson 1922a: 110-111).

Turesson's views on speciation conflicted with the mutationist theories of De Vries and Johannsen and with the hybridization theory of Lotsy (cf. Turesson 1922b, 1929). Turesson accepted that hereditary types existed within the species, but to call these types themselves species is "to strip the ordinary species, as found in nature of one of its most characteristic properties viz. the ability to respond genotypically to a wide range of different habitats with such units or habitat types, representing various combinations of Mendelian factors" (Turesson 1922b: 342).

It was also a theory of speciation at variance with the neo-

Lamarckian position advocated by Hall and Clements. In a discussion of the latter's work Turesson (1925: 230-231) welcomed their use of experimental methods in taxonomy but he criticised the claim that environmental variation could become directly fixed into the genotype of the plant. Hall, after he had begun his own series of transect experiments in California, visited Turesson at Lund. The possibility of joint research projects was considered, but difficulties involved in connection with the shipping of plant materials led to a postponement of this venture and no joint research was ever undertaken.¹⁹

For the study of ecospecies and ecotypes Turesson coined the term genecology. This was defined as "the study of species and their hereditary types as related to environment" (Turesson 1923: 171). As such genecology was a branch of ecology, comparable to synecology and autecology.²⁰ However, from the very start, Turesson also saw genecology as a discipline which would replace orthodox systematics. Turesson argued that an ecological understanding of speciation involved a different conception of the species from that employed in traditional systematics:

That the genecological units do not necessarily - and probably quite often do not - coincide with the Units of the traditional systematics is quite clear. The divergences are due to a large extent to different conceptions of the species. The point of view of the genecologist - that the species represent an intercrossing community, the members of which have secondarily become clustered into groups (viz. ecotypes) on account of the differentiating effect of environmental factors upon the genotypically heterogenous population - is very different from the systematists view of species. From the point of view of traditional systematism a species is composed of forma genuina and deviations are subordinated under this type as varieties and forms of "less systematic" value. Apart from the untenability of this view, the supposed type may include a number of ecotypes, and several varieties may conversely be found as normal constituents forming parts in one and the same ecotype, as has been shown in my previous work.

(Turesson 1925: 173)

The clearest statement of Turesson's views on traditional systematics was put forward in a paper entitled "Genecological Units and their

19. The correspondence between Hall and Turesson has been preserved in the Turesson archives at Lund.

20. Autecology is the study of individual species, synecology the study of the plant community.

Classificatory Value", (1930). From this paper it is clear that Turesson viewed genecological units as a rival to the categories employed by orthodox taxonomists. Orthodox taxonomy is at best a kind of necessary preliminary to experimental investigation. The classifications it produces are artificial and thus of little service to most biologists. Genecological categories, in contrast, are seen as being based upon the naturally occurring phenomena of ecological differentiation and are thus real:

Systematics of the purely descriptive kind do not provide the instrument by which the cause and nature of group phenomena in organisms may be investigated, nor do systematics of this kind furnish the adequate means of determining the natural boundaries of the groups. While it is true that classification might be made without any such means it is equally true that a classification of this kind must be considered as mere preliminary and be of limited scientific value.

(Turesson 1930: 511)

In his early research Turesson applied his ecotype concept solely to plant species which reproduced wholly, or partly, by means of sexual reproduction, i.e. amphimictic species. However, later research with groups that were asexual or apomictic in their breeding convinced Turesson that the ecotype concept could also be applied in these cases (Turesson 1926, 1943). The result of this new line of research was that Turesson twice redefined and substantially modified his definitions of the ecospecies and the coenospecies (Turesson 1929, 1943). Thus, in the 1929 paper, a distinction was made between sexually reproducing ecospecies which can be defined in genetical terms and apomictic agamospecies which cannot. Ecospecies, thus redefined, become "an amphimict-population the constituents of which in nature reproduce vital and fertile descendants with each other giving rise to less vital, or more or less sterile descendants in nature, however when crossed with constituents of any other population" (Turesson 1929: 333). Apart from widening the scope of populations to which the genecological terminology could be applied, this redefinition of the term "ecospecies" had important implications for later developments in biosystematics. Ecospecies and ecotypes had originally been used as ecological terms but after 1930 most workers, including Turesson himself, came to regard these units in genetical terms. For many later workers ecological species were "ecological"

only insofar as partial or total genetic isolation is often accompanied by ecological separation. The desirability of using Turesson's genecological hierarchy in this manner is still a matter for dispute amongst both taxonomists and biosystematists (cf. Heywood 1959 and Valentine and Löve 1958).

Not all ecologists were willing to accept either that species had to be defined in genetical terms or that recombination and natural selection were the methods by which new species arise in nature. In Sweden the strongest opponent of Turesson's new genecology was not a taxonomist but a fellow ecologist, Gustaf Einar Du Rietz. Du Rietz was a phytosociologist and his major research concerned descriptive studies of the Swedish and Norwegian mountain and moorland vegetation. However, he also contributed one major paper on "The Fundamental Units of Biological Taxonomy" (Du Rietz 1930) which was widely cited by later biosystematists. In effect this article was an attempt to reconcile the terms and methods of traditional taxonomy with the more modern experimental approach. Du Rietz was critical of traditional taxonomy and stated that "the pure abstraction method of species-making by sorting specimens into groups merely after their morphological resemblance as still practised by many taxonomists (and still supposed by Lotsy and many other geneticists to be the method of all taxonomy), must be firmly rejected" (Du Rietz 1930: 387). Du Rietz, like Turesson, was convinced that taxonomists must change their methods, but in a way very different from that recommended by Turesson. For Du Rietz the salvation of taxonomy lay in what he called the "morphological-geographical method", a combination of the methods of herbarium taxonomy and descriptive field ecology. Species were defined by Du Rietz in morpho-geographical rather than in genetic terms, as "the smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotypes" (Du Rietz 1930: 357). Old orthodox taxonomical units such as "subspecies" and "variety" were retained, and Du Rietz was critical of the use of new terminologies like the genecological system, which he deemed to be unnecessary (Du Rietz 1930: 361). Du Rietz did not deny the importance of data from transplant experiments, but he saw the results thus obtained as subordinate to the study of wild populations :

If we take home a single specimen or a few specimens of each species, of each subspecies or even of each variety of a genus, plant them in our gardens, cross them with each other and play with them in various ways, they will still tell us nothing about the variability of polymorphy in the wild populations concerned, i.e. nothing of what is most essential for grasping the species and their subordinate units. The field study of the variability of polymorphy of wild populations can be replaced as little by the study of a few living individuals brought home to a garden as by a few dry individuals in a museum, and it is often more use to get a number of dry individuals, sufficient for getting at least some idea of the variability of polymorphy in the wild population than it is to get an insufficient number of living individuals to a garden. The claim of Turesson and other geneticists to have replaced the old "descriptive taxonomy" with a new "experimental taxonomy" must therefore be firmly disputed.

(Du Rietz 1930: 388)

In fact, the disagreements between Du Rietz and Turesson extended beyond the realms of species definitions, terminology and methodology. Du Rietz was unconvinced that selection could be the sole agent in evolution and felt that Turesson's genecology overemphasised its importance (Du Rietz 1930: 399-400, 410 and see also Goddijn 1934: 84).

Turesson's reply to Du Rietz was written in conjunction with two other Lund geneticists, Arne Muntzing and Karl Olaf Tedin. Muntzing (1930) had already published a monograph employing Turesson's terminology and methods to the genus Galeopsis. The Lund authors criticised the work of Du Rietz on a number of issues. His species concept was attacked as being subjective and no advance on the morphological species definitions already employed in traditional systematics. The authors also defended the use of genecological terms: "ecospecies" and "coenospecies" which Du Rietz had claimed were practically synonymous with the term species if the latter was properly defined. And, finally, there was a critique of Du Rietz's comments concerning the role of selection in speciation. The Lund authors ended their paper by quoting a passage from Du Rietz in which he argued that "the role of selection has been much overrated ... It mainly consists in the elimination of biotypes absolutely unviable in a certain habitat" (Du Rietz 1930: 399), and they commented that opinions such as these appear to demonstrate that

... for the solution of the problems (of evolution) here discussed experimental playing in the garden with plants

has proved its superiority over field studies, be the latter combined with an ever so skilful playing with words.

(Müntzing, Tedin and Turesson 1931: 16)

This controversy was not the first time that Turesson and Du Rietz had clashed. In an earlier paper Turesson had already criticised Du Rietz's assertion that species found in a large number of variable plant associations do not respond to the different ecological factors in each association by the production of ecotypes (cf. Du Rietz 1923; Turesson 1925: 232-233). The personal animosity between the two men was also increased by the fact that both had applied for the professorship of botany at Lund University.²¹ However, the work of Du Rietz is worthy of note for two reasons. Firstly, it shows that even by 1930 the issue of what role selection plays in evolution was still a matter of contention between ecologists and geneticists. And, secondly, it shows that taxonomists were not alone in their distrust of experimental methods; at least some ecologists also felt that classification should not rely on experimental and genetic criteria.

Although Turesson's views on taxonomy received a mixed reception from taxonomists and some ecologists, the ecotype-terminology quickly became established as the major classification system of experimental taxonomy. The way in which Turesson's research was taken up and modified by subsequent workers forms a dominant theme of Chapter 5.

Discussion: The Species Concepts of Clements and Turesson

Clementsian taxonomy had two major objectives:

1. to get back to the broad morphological species of Linnaeus.
2. to show that variation exists within the Linnaean species as a result of the action of external forces in the environment on the plant's growth and heredity.

It was to demonstrate the latter claim that Clements performed transect experiments. Clements believed, following Bonnier, that species transformation from one kind to another would take place under the action of such environmental change. Indeed, Clements maintained this belief in the power of speciation by direct adaptation throughout

21. Neither, in fact, obtained the post.

all his working life.

The use of broad morphological resemblances meant that the species of Hall and Clements often overlapped in practice with the species of the older "Linnaean" taxonomists of the herbarium. However, this overlap is, in many ways, coincidental. The principles behind which the Clementsian approach to speciation is based is radically anti-Linnaean. For Clements there are no special features of a species which defines its essence; indeed species will transform from one kind to another given the right environmental circumstance. Instead the emphasis is on species as changeable, malleable entities. This emphasis on the dynamical and historical is evident in Clements' writings in ecology as well as taxonomy. Indeed the parallel is one to which he himself referred:

It would be entirely superfluous to state that the major difficulty in the analysis of vegetation is its complexity, were it not for the fact that it is too often taken as the warrant for the static viewpoint. This was embodied in the original idea of the formation as a unit in which communities were assembled on a physiognomic basis, quite irrespective of generic composition and phyletic relationship. It is not strange that this view and its corollaries should have persisted long past its period of usefulness, since this is exactly what happened with the artificial system of Linnaeus, but the time has come to recognise fully that a natural system of communities must be built just as certainly upon development and consequent relationship as must that of plant families.

(Clements 1936: 282)

Clementsian species are not classified on the basis of permanent features or essential characters, either in the genotype or phenotype. Indeed for Clements such permanent features of a species do not exist: ultimately any apparent stability of species in nature is only a feature of the relative stability of the habitat in which the plant is growing. As a result Clementsian taxonomy works in a way which is completely at variance with Putnam's account of scientists as seeking out essences of natural kind terms and using these as rigid designators. For Clements the cluster of morphological properties on which, as a matter of necessity, species-making has to depend are more like identifying descriptions or stereotypes. These properties are a guide to classification of species but they cannot be used to locate the essence of a natural kind because for Clements there quite simply

are no such essences.

The problems inherent in Putnam's account of natural kind terms and their usage is also well illustrated by the fate of De Vries work on Oenothera during this period. According to Putnam a words usage is fixed by its "christening", which then provides the paradigm instance of its use. De Vries clearly expected his use of the concept of mutation to be taken in this way: it was presented as a detailed account of the nature of speciation in one group (Oenothera) but as a theory which later research would show to be of general applicability. In fact however two things happened:

1. Experimental taxonomists who were opposed to mutation as a general theory of speciation (e.g. Clements) accepted his work as proven for Oenothera but denied its general applicability.

2. Ultimately research by B.M. Davis, R.E. Cleland and others showed that "mutation" in oenothera was not in fact mutation but rather that the variation observed could be explained as a complex form of permanent heterozygosity. The usage of the terms "mutant" and "mutation" still conformed to De Vries' description of mutation as change in genetic substance, but the paradigm case of mutation was rejected on the grounds that it did not match this verbal description. In this instance at least the terms later usage does not appear to have depended on the initial referent. A fully elaborated casual theory of reference might be able to overcome a counter-instance of this nature. But, at the moment, it would appear to be a case which, if anything, fits the Fregean model of reference as achieved by description rather than causal usage.

Turesson's employment of the term species shows discrepancies with both description theorists and essentialists views on natural kinds. For Turesson there are 3 kinds of species viz. ecospecies, coenospecies and agamospecies. Ecospecies are defined in genetical terms. Members of an ecospecies are variable in both their phenotype and genotype but are bound together by a same-essence relationship which refers to breeding behaviour. All members of an ecospecies are potentially capable of crossing and producing fertile offspring.

But, defining species in this manner raises two problems. The

first of these is that a limited amount of gene-exchange may occur between members of different ecospecies. This, for example, may occur when two ecospecies which are normally separated by ecological and geographical barriers occasionally meet in areas and habitats where their ecological preferences overlap. Such rare crossing of this sort which does not indicate complete fertility of the two species involved can even take place on occasion between different genera:

By definition a coenospecies includes all types which are united directly or indirectly by crossability and which may exchange genes. In extreme cases such as coenospecies may comprise ecospecies from different genera.

(Müntzing 1935: 57, emphasis added)

The coenospecies then, overcomes the first problem.

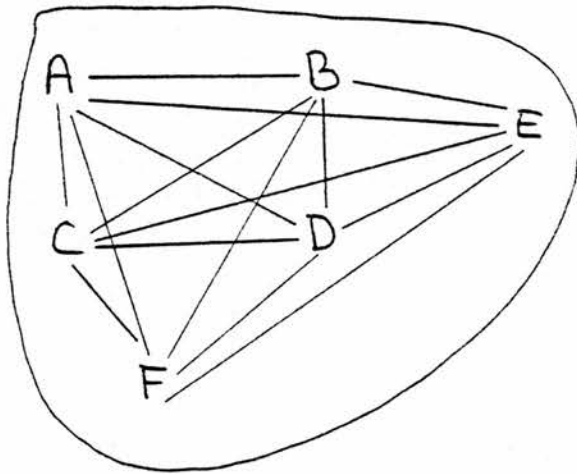
The second problem of defining species by means of genetical behaviour is that such a definition is only applicable in groups where sexual reproduction takes place. Apomictic plant species are not species if this definition is adhered to. To cover cases of this sort Turesson introduced the term "agamospecies", the latter being defined as:

An apomict - population the constituents of which for morphological, cytological and other reasons, are to be considered as having a common origin.

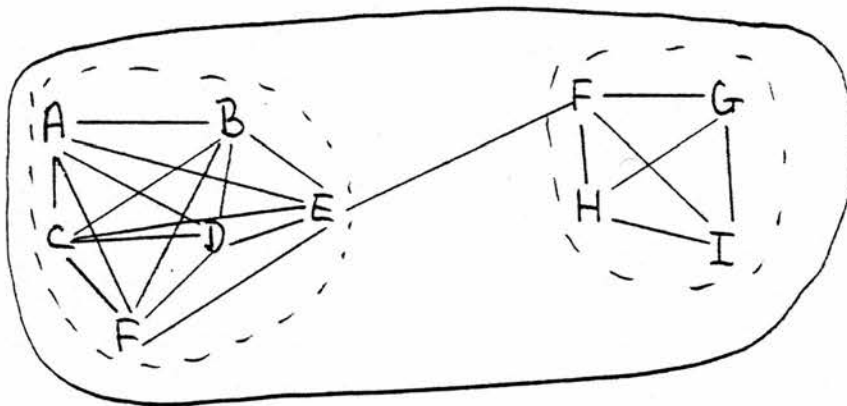
(Turesson 1929: 333)

These three terms are illustrated diagrammatically in figure 4.3. As is evident from that figure, ecospecies in principle, at least, have an extension which is favourable in terms of a same_e relationship of reproductive behaviour. If A is the first known instance of an ecospecies X then all subsequent members will be able to cross with A and produce more-or-less fertile offspring. However, no such same_e relationship binds together the members of a coenospecies. Two plants may be unable to exchange genes directly but still be members of the same coenospecies. And in practice Turesson recognises coenospecies on the basis of a series of identifying descriptions. Coenospecies have "a common origin so far as morphological, cytological or experimental facts indicate such as origin" (Turesson 1929: 333). Agamospecies are also defined in this way. There is no essence which decides membership of an agamospecies. Rather, a cluster of morphological

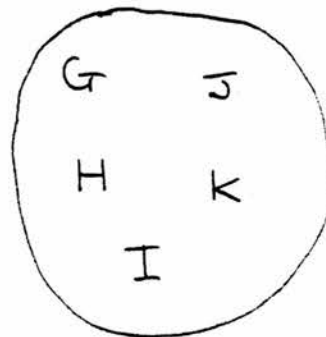
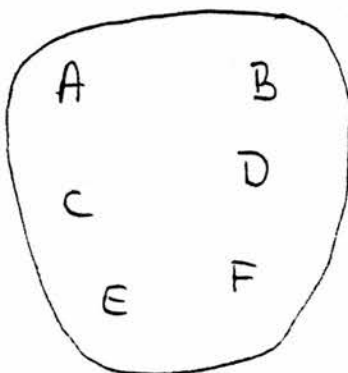
Figure 4.3. Ecospecies, Coenospecies and Agamospecies.



Ecospecies: all members interfertile



Coenospecies: gene exchange possible but highly restricted



Agamospecies: no gene-exchange

and cytological properties are used to decide membership.

Clearly, essentialist and descriptivist accounts of classification show not how scientific classifications must be made but rather, two different strategies by which they might be made. Not only are both possibilities concurrent with some science, both strategies may be incorporated into the work of a single scientist. Turesson's work indicates superbly the limitations of both models as general accounts of the classification process in science.

Genetic criteria have often been employed since either to delimit species or to demarcate different kinds of species. However, there remains no universal agreement concerning their use. For example, Heywood in a recent paper has strongly criticised the way in which genecological units have become "the property of geneticists" (Heywood 1959: 91). And, more generally, Rollins has argued that genetical criteria are inadequate as a definition of the species:

To insist on infertility (incompatibility) as the sole criterion of species ignores the aims and methods of taxonomy and seeks to make taxonomy subservient to a condition - sterility in genetics, by raising it to the importance of a universal principle.

(Rollins 1953: 181)

These controversies suggest that Turesson was only partly successful in forging a synthesis between ecology and genetics, with respect to the experimental classification of plants. In the period after 1930 most biosystematists were cytologists and geneticists, and their treatment of the genecological system naturally reflected cytological and genetical concerns.

The connection between experimental taxonomy and ecology means that the early history of the discipline cannot be considered in isolation from the events which were taking place in ecology itself during this period. Stress on the need for experimentation and quantification of data were common in the writings of plant ecologists during the first three decades of the century and reflected, in part at least, the newly emerging status of ecology as a profession. Ecological studies were no longer to be the province of the amateur natural historian but the professional scientist. For these ecologists,

by analogy, the way forward in taxonomy was also seen as linked to the adoption of experimental and quantitative techniques.

The early experimental taxonomists were highly critical of traditional systematics and saw their own discipline as one which would eventually replace orthodox taxonomy. They believed that the classifications of experimental taxonomy were superior to those which could be produced by orthodox taxonomists and that the latter was, at best, a mere preliminary to proper experimental investigation.

By the early 1930's Göte Turesson's genecological terminology had become the most important of the systems of classification available to experimental taxonomists. Much of the work which took place in experimental taxonomy after this period can be seen as an extension, elaboration and refinement of the genecological classifications and techniques first expounded by Göte Turesson.

Chapter Five : Experimental Taxonomy and Genecology 1930-1950

The period around 1930 saw the initiation of several crucial changes in the scope, aims and direction of experimental taxonomic research. One of the most important of these changes was the increasing use of cytogenetical methods and concepts. From 1920 to 1930 most of the major research in experimental taxonomy had been carried out by men whose backgrounds were in ecology. In the period after 1930 geneticists and cytologists became more prominent in the advocacy of an experimental approach to classification. The interest of geneticists and cytologists in the species concept can be seen from the discussion of that topic held at the fifth International Botanical Congress in Cambridge (England) in August 1930. That discussion was dominated by cytologists and geneticists: figures present included E. Anderson, E.B. Babcock, J.P. Lotsy, C. Darlington, E. von Tschermak (one of the rediscoverers of Mendel's work) and the Russian plant breeder N.I. Vavilov (see Table 5.1). Turesson and Du Rietz also were present at the conference but they gave their papers to a separate symposium which discussed geographical distribution and its relationship to the species concept.

A second change apparent after 1930 was a shift in theoretical interest. From 1900 to 1930 the major theoretical concern of experimental taxonomists had been to test out different theories of speciation by using transplant techniques. In the post-1930 period the controversy over the mechanism of speciation was seen as resolved, in favour of the selectionist viewpoint advocated by Göte Turesson.¹ The major theoretical issue in research after 1930 focused on the question of what kind or pattern of variation resulted from the action of selection on intraspecific variation. Turesson, and later Clausen, held that such variation was discontinuous in nature, a reflection of the discontinuous nature of the habitat itself. For Turesson and Clausen ecological variation within the species was a mosaic describable in terms of ecological types. However, in the 1930's several important schools of genecological thought developed which challenged this interpretation and argued that ecological variation within the species was

1. Although the possibility that environment directly acted to produce new species was re-opened by the developments in Russian biology under Michurin and Lysenko (see Mather 1942).

Table 5.1. Speakers at the Discussion on the Species Concept held at the 5th. International Botanical Congress, Cambridge (information from Brooks and Chipp 1931).

H. H. Allan	Ecologist	New Zealand
E. S. Anderson	Geneticist	U.S. A.
E. B. Babcock	Geneticist	U.S.A.
C. D. Darlington	Geneticist	U.K.
E. W. Erlanson	Cytologist	U.S.A.
M. L. Fernald	Taxonomist	U.S.A.
F. Gagnepain	Taxonomist	France
A. L. Hagedoorn	Geneticist	Netherlands
D. Hall	Agricultural botanist	U.K.
J. W. Heslop-Harrison	Taxonomist	U.K.
A. S. Hitchcock	Taxonomist	U.S.A.
C. C. Hurst	Geneticist	U.K.
T. J. Jenkin	Taxonomist	U.K.
J. P. Lotsy	Taxonomist	Netherlands
C. H. Ostenfeld	Cytologist	Denmark
C. F. L. Tischler	Cytologist	Germany
E. von Tschermak	Geneticist	Austria
N. I. Vavilov	Plant breeder	U.S.S.R.

continuous or clinal in nature. This interpretation initiated a debate which is still unresolved.

Thirdly, the period after 1930 also witnessed a change in the way experimental taxonomists came to perceive the relationship between their discipline and that of orthodox taxonomy. In the period from 1920 to 1930 experimentalists had seen their discipline as one which embodied techniques and results which would come to replace the existing practices of the orthodox school. However, in the period after 1930 many experimentalists came increasingly to stress that experimental taxonomy was an addition to, rather than a replacement of, orthodox systematics. Indeed, some even went further than this and maintained that experimental "taxonomists" should give up their pretensions to being engaged in a classificatory activity at all and concentrate instead solely on elucidating the mechanisms and pathways of microspeciation. This debate too has remained unsolved.

In this chapter these changes will be considered in more depth. However, it will be pertinent to begin by examining briefly the wider context of changes in biological research that were manifest in the 1930's and 40's. For it was a response to these wider developments that many changes in genecological thinking can be in part related.

Biological Research in the 1930's and 40's: The Emergence of the Synthetic Model of Evolution

Biological theory in the 1930's and 40's was dominated by the emergence of the so-called 'synthetic' model of evolution. The approximate dates for the emergence of this view can be obtained by listing the major publications of this school: Dobzhansky 1937; Huxley 1940, 1942; Mayr 1942; Simpson, 1944, 1953; Stebbins 1950. The new interest in evolutionary matters can also be discerned in the emergency in 1947 of the journal Evolution.

The adherents of the synthetic model of evolution sought to use evolutionary theory as the corner-stone of integrating the diverse disciplines of twentieth-century biology. The foundation and starting point for such an enterprise was undoubtedly the realisation of the mutual compatibility of Darwin's theory of natural selection through

the inheritance of small continuous variations with Mendelian particulate genetics. The basis for this synthesis had been forged in the decade between 1910 and 1920 through the work of geneticists such as Castle, East, Nilsson-Ehle and Morgan. However, the later research of Dobzhansky, Mayr, Simpson, and others was concerned with more than demonstrating the mere compatibility of Darwinism and Mendelism; it was an attempt to place all the disciplines of biology, including genetics, cytology, biogeography, paleontology and taxonomy within an evolutionary framework.

The question arises of why this 'grand synthesis' (as Mayr termed it) did not take place until the late 1930's and 40's. If Provine is correct in his claim that "in 1918 ... many geneticists accepted Mendelism and Darwinism as complementary" (Provine 1971: 129), why was there no synthesis during the decade from 1920 to 1930?

Part of the answer to this problem lies in recognising that the synthetic model of evolution proceeded not in one but in two steps. The first of these was the combining of the research programmes being carried out in experimental Mendelian genetics and the mathematically orientated biometry of such figures as Pearson. This took place in the period after 1918. The second phase of the synthesis was the merging of the experimental disciplines of genetics and cytology with the 'naturalist' tradition in biology evident in the disciplines of taxonomy, biogeography and ecology. It was this second phase which was not begun until the late 30's and which was not fully completed until after 1950.²

The attempt to provide Mendelian genetics with a mathematically based model which would account for the flow of genes through a population had a long history. In retrospect, the origins of this endeavour can be traced to the work of G.U. Yule (1871-1951) which was begun as early as 1902. But, at the time Yule was writing, his views were very much an exception to the general trend. Most mathematically orientated biologists prior to 1910 had, following the path of the leading British biometrician Karl Pearson (1857-1936), rejected particulate theories of inheritance in

2. The rise of neo-Darwinism and the emergence of population genetics has been the subject of a recent study by Provine (see especially Provine 1971) and it is from this source that much of the following account has been derived.

favour of the non-particulate theories of Francis Galton. The experimental work of Morgan, Castle and Nilsson-Ehle brought about a change in this position and most mathematical biologists after 1918 began to set about the task of demonstrating a quantitative proof of the operation of selective processes on units of Mendelian heredity in animal and plant populations.

The leading exponent of this synthesis of biometry and Mendelism, was R.A. Fisher (1890-1962). Fisher had come to the opinion that biometrical results could be explained in terms of Mendelian inheritance as early as 1918, although the full presentation of his arguments was not made until 1930 (Fisher 1918, 1930). Other prominent figures in the mathematical investigation of Mendelian heredity and selection were Sewall Wright (1899-) and J.B.S. Haldane (1892-1964). The result of this research was that by 1930 there was little doubt that the findings of experimental geneticists working on Drosophila and other laboratory organisms could be accounted for by a mathematical model of population genetics centred on the key notion of selection. However, the details of this model were still a matter of controversy and have continued to remain so.³

The analyses of Fisher, Haldane and Wright were largely of a theoretical nature and based on laboratory experiments rather than on studies of the genetical and cytological characteristics of wild populations. And, as a result, their studies underemphasised the importance of factors like the high variability of natural populations, gene interaction and recombination (Mayr 1973: 126). The second phase of the grand synthesis was concerned with assimilating the quantitative and experimental data of theoretical population genetics with data on natural populations. But this step was not taken until after 1935.

However, in retrospect, this second phase in the emergence of the synthetic model of evolution can be seen to have had its intellectual roots in the work of Russian biologists which was done prior to 1930.

3. These difficulties stem from the different evolutionary interpretations of Haldane, Fisher and Wright. Fisher emphasised the effect of small selection pressures acting over long periods of time. Wright and later workers such as Mather emphasised the importance of genic interaction. For a discussion of the writings of Fisher, Haldane and Wright, see Provine (1971: 130-178).

The most important of these Russian biologists was S.S. Chetverikov (1880-1959) who, with his students N.P. Dubinin, N.V. Timofeev-Resovsky and T. Dobzhansky, was employed in the genetics section of the Institute of Experimental Biology in Moscow.⁴ Chetverikov was an entomological taxonomist by training, who only turned later in his life to an interest in biometry, genetics and the theory of evolution. From 1922 to 1929 he and his co-workers began a series of experiments on the genetics of wild populations of Drosophila. These workers stressed, as Nilsson-Ehle had done with his research on maize, the enormous importance of genetic or "hidden" variability in wild populations due to the presence of recessive alleles. Chetverikov correctly concluded that this must be an important source of variability on which selection could operate. The Chetverikov school also stressed the importance of gene-interaction in producing phenotypic variation and the phenomena of the "genotypic milieu". Underlying this research on the biometry and genetics of Drosophila were a number of crucial assumptions drawn from the writings of "naturalist" orientated zoologists such as Karl Jordan and John T. Gulick.⁵ In particular Chetverikov assumed that zoological species were real entities which could be defined in terms of capacity to interbreed successfully and produce fertile offspring, and he stressed also the role of isolation in speciation.

The evolutionary thinking of Chetverikov, Dubinin and Dobzhansky achieved the basis for an integration of experimentalist and naturalist-orientated studies focused on wild populations of animals and plants. In the West the work of Dobzhansky, who had emigrated to the U.S. in 1927, became particularly closely associated with this synthetic approach. It was a view which at first was more closely allied with zoology than botany: Mayr, Simpson and Huxley were all zoological systematists by training.

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4. The contributions of Chetverikov and the Russian school to population genetics is discussed at length in Adams (1968, 1970). It is from this source that the present account is taken.
 5. This is most evident in Chetverikov's concept of speciation. He held that the creation of new species was independent of adaptation. Speciation was to be explained in terms of isolation; subsequent adaptations in terms of natural selection. This theory of speciation, which entails the formation of new species without selection, Adams (1970: 110-112) attributes to the influence of Gulick.

However, in the long run, as Stebbins work showed, it was a perspective applicable to both animal and plant populations. The picture which finally emerged was an evolutionary model of speciation which emphasised the role of mutation, recombination, isolation and natural selection acting together to produce new species. And the task of assessing the importance of each of these forces in any one instance was seen as involving, of necessity, a combination of approaches centred on the techniques of systematics, bio-geography, genetics, cytology and mathematics.

The significance of the synthetic model of evolution for systematists was that it provided a new and expanded role for taxonomic enquiry. Taxonomy of the new experimental kind was a central pillar in the new synthesis of genetics, evolution and ecology. The proponents of the "new systematics" were anxious to dispel the negative image of taxonomy held by most laboratory investigators. Mayr (1942: 3) spoke with regret of the contempt of the laboratory worker for the museum man who spends his time counting hairs or drawing bristles. But the systematist in turn would have to see his work in a new light:

(T)he new systematist tends to approach his material more as a biologist and less as a museum cataloguer. He shows a deeper interest in the formulation of generalizations, he attempts to synthesize and to consider the describing and naming of a species only as a preliminary step in a far-reaching investigation.

(Mayr 1942: 7).

For Mayr concern should be focused on classification of subdivisions within the species. The population is the basic unit of taxonomy. The purely morphological species concept is replaced by a biological definition; "species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr 1942: 120). Nomenclature is no longer to be a central concern for the taxonomist and the material the systematist studies will have to be sufficient to take account of individual variation within the species (Mayr 1942: 7). The new systematist wants to know how species originate and how they are related; for him systematics is more than the "mere pigeonholing of specimens" (Mayr 1942: 9). And this course of action was recommended as the obvious way to save

taxonomy from the status of neglect, obscurity and disrepute into which it had fallen compared with the new, more experimental, disciplines of biology.

These writings supported many of the criticisms which experimental taxonomists had been making about orthodox taxonomy during the previous two decades. Experimental taxonomists in the 1930's and 40's were quick to take up the challenge offered by the "new systematics" which they themselves had in part helped to formulate. Also, the success of the neo-Darwinists such as Dobzhansky, Mayr and others was a triumph for the evolutionary views pioneered by Turesson in the 1920's. The influence of Turesson's work was nowhere more apparent than in the large-scale transplant experiments carried out by Jens Clausen and his colleagues in California. Indeed, Clausen's work represents the most thorough and complete research on genecological differentiation which has ever been undertaken. It is therefore necessary that any account of experimental taxonomy during the 1930's and 40's should begin with an account of this research.

Jens Clausen and the Second American School of Experimental Taxonomy

Jens Clausen was born at Eskilstrup, Denmark in 1891. Educated at the University of Copenhagen from which he obtained a Ph.D. in 1926, Clausen was for ten years (1921-1931) an assistant to the Danish cytologist and geneticist Øjvind Winge at the Department of Genetics of the Royal Veterinary and Agricultural High School in Copenhagen. In 1931 he emigrated to the U.S., where he joined Harvey Monroe Hall's team at Stanford, working under the patronage of the Carnegie Institute of Washington. After Hall's death in 1932 Clausen was put in charge of a special section for experimental taxonomy and in 1951 he was appointed professor biology at Stanford University. Clausen became a naturalized U.S. citizen in 1943. He died in 1969, at the age of 78.⁶

The discussion of Clausen's work which follows is divided into two parts. Part one considers the work which Clausen did prior to his emigration to the U.S. in 1931. This is followed by a discussion of the research, mostly done in conjunction with David Keck and William

6. These biographical details of Clausen's life are taken from an obituary by Böcher (1970).

Hiesey, undertaken in California.

Clausen's contribution to experimental taxonomy prior to 1931 consisted of a series of papers concerned with the cytology, genetics, ecology and taxonomy of Viola tricolor and its related species. The cytogenetics of this group is complicated, chiefly because populations of Viola tricolor and Viola arvensis tend to hybridize where their respective geographical ranges overlap. An indication of the diverse interests which Clausen was concerned with in his research can be seen from the first of the papers on Viola in which Clausen defined the principle objectives of his research as comprising:

1. Decomposition of the species into elementary species;
2. The relationship to other species of the Melanium section of the genus Viola;
3. Cytological investigations, and
4. The problem of heredity.

(Clausen 1921: 205).

Clausen's early work had affinities with the early work of Turesson. Clausen was convinced that genetical data must be employed in taxonomy; he referred in the 1921 paper to "the chaotic state, that would be the result, if we persisted in applying the old Linnaean definition of the species in this Mendelian age of ours" (Clausen 1921: 213). Like Turesson, Clausen made a strong distinction between variation which was due to heredity and that which was due solely to the action of the environment, although he employed a different terminology to mark the distinction.⁷ And Clausen, like Turesson, specifically rejected Lamarckian explanations of the relationship between environment and speciation; new types are selected and not created by the environment (Clausen 1922: 407-410).

Like other experimental biologists writing during the 1920's on matters of concern to systematics, Clausen was highly critical of what could be achieved by the traditional methods of orthodox taxonomy. In a 1922 paper on Viola Clausen concluded that:

7. In the 1921 paper Clausen refers to genetic strains within a species as "micro-species".

The splitting up of the Linnaean species ... has frequently been based upon accidental observations of deviating individuals which are described, instead of trying to make a perspicuous classification of the types within the species based upon studies in the extent and the cause of the variation and other questions in connection herewith. In many cases this result is due to the fact that these systematists either do not accept the consequences of, or are not fully familiar with all the results of modern biology. The systematist's investigations are so difficult that it is needful that he uses all the resources at his disposal. At the investigation of the small systematic units within the single Linnaean species he cannot be content with employing the old methods alone, which suited the classification of the Linnaean species themselves long ago.

(Clausen 1922: 397)

And Clausen was especially contemptuous of results in groups like Viola and Hieracium where hybridization is a common phenomena.

Clausen's early views on traditional methods of taxonomy are also reflected in his writings on the species problem during this period (see Clausen 1927). Clausen was not a firm advocate of the biological or genetic species concept. His research on Viola had shown that species could produce fertile offspring but still have different chromosome numbers and remain distinctive over most of their geographical range. Indeed, he conceded that the delimitation of species was, partly at least, a matter of convenience rather than of biological necessity. But, he argued, it was precisely because there was room for personal judgment in critical cases that the taxonomist must rely on investigations drawn from as many different fields of enquiry and research as possible:

The frequent establishment of species of doubtful value is very largely due to their being based principally upon herbarium studies. The specimens of the herbaria represent but a small selection from the abundance of nature. It is very easy to keep a few so-called species or varieties separate as long as one is working only with herbarium specimens; but the units of classification thus established are of no use whatever in the field, as has already been pointed out by Hall and Clements. Nature is infinitely richer than the herbarium would seem to show.

(Clausen 1927: 706).

One question which Clausen tried to answer concerning the Viola tricolor-arvensis complex was whether there existed in this group intraspecific variation which could be explained as a genetical response to different ecological habitats. Clausen's conclusion, based upon both morphological data and on transplantation of plants into a standard

habitat, was that such genecological variation could be found in this group (Clausen 1922: 407). However, most of Clausen's research on ecological races within the Linnaean species was undertaken after his move to California in 1931.

As was shown in Chapter 4 the experiments in California had been started by Hall and his co-workers, Keck and Hiesey, in 1922, in an attempt to study elements of the Californian flora by the same methods that Hall and Clements had used previously during studies at Pikes Peak in Colorado between 1918 and 1921. However, by 1931 Hall had become convinced that Clements' theories of adaptation and ecogenesis could not account for the results which were being obtained in California and that the environment was selecting types rather than directly influencing changes in the populations of plants under study. Clausen's work confirmed this view and showed that non-inheritable modifications to the plant's phenotype due to environmental transplanting were usually of a minor order, and of a temporary nature, being reversible if the plant was returned to its old habitat. No evidence was found of environmental factors inducing yearly cumulative effects upon the growth of perennial transplants (Clausen, Keck and Hiesey 1935: 201).

The objectives of this research remained two-fold (Clausen, Keck and Hiesey 1932: 201): to make a contribution towards "a rational and complete classification" of the plant taxa studied and to further an understanding of the processes operative in the development of these taxa. There is no evidence that Clausen or his colleagues saw any incompatibility in these two aims; they were complementary aspects of the new discipline of experimental taxonomy.

The methods used to achieve these two ends were diverse. In the first of their classic series of papers Clausen and his co-workers (Clausen, Keck and Hiesey 1932: 202) listed their methods under six headings: 1. Field studies (of geographical distribution, habitat preferences etc.); 2. Experimental transplants; 3. Comparative morphological studies using herbarium and living material; 4. Cytological and anatomical studies; 5. Genetical analysis, i.e. artificial hybridization and breeding tests; 6. Synthesis of these results. The Californian team was in a good position to carry out such studies

because there was a division of labour within the group: Clausen's background was in cytology and genetics; Keck was a taxonomist; Hiesey an ecologist and physiologist. This diversity of approaches was reflected in the principle, enunciated many times by Clausen and his co-workers, that problems of plant evolution and systematics required understanding from a plurality of perspectives if success was to be achieved in their solution:

Genetics and cytology are not the ends but auxiliary disciplines, being subordinated to the study of relationships and evolution of the systematic units of plants. Likewise morphology, plant geography and ecology are brought into harmony with the present day cytogenetical principles, based upon them and correlated one to the other. It was felt that the key to an understanding of relationship and evolution was to be found not in any single one of these principles but in all of them together.

(Clausen, Keck and Hiesey 1936: 209).

The major type of transplantation technique used by Clausen and his group was of the kind known as "clone transplanting" (Clausen, Keck and Hiesey 1940: 16-18). In this method the plant chosen for experiment was dug up, given an experimental number, and a sample of it taken as an herbarium specimen. The plant was then propagated vegetatively and each propagule, when ready, used in the actual transplant gardens. Although Clausen and his co-workers sometimes cultivated population samples side-by-side in a standard garden as well, this was not the major method employed (cf. Clausen, Keck and Hiesey 1940: 4). The use of clone transplants had several advantages over the standard cultivation technique which Turesson had employed. The most important deficiency in the latter method is that in eliminating environmentally imposed variation it may obscure genetically determined differences in the capacity to react adaptatively to special environments. Also, the test environment, while suppressing some environmentally induced characteristics, may evoke others never expressed in the natural habitat. Clone transplanting overcomes these deficiencies in the standard garden transplant technique.

The transplant experiments of Clausen's group were undertaken on a scale which has never been repeated. The basic transect line used stretched across nearly 200 miles of central California. Along this transect line three major gardens were established at 100 ft. (Stanford),

4,600 ft. (Mather) and 10,000 ft. (Timberline). A relief map showing these locations and the transect on which they were situated is shown in figure 5.1. These three transplant stations covered a wide range of climatic conditions. At Stanford near the Pacific coast the weather is mild and conditions are favourable for plant growth over most of the year. At Timberline there are normally only three to six weeks of frost-free weather in the summer during which plant growth is possible. At Mather conditions are intermediate between these two extremes. In addition to the wide range of climatic differences at these three locations Clausen and his team also set up gardens to test the effects of moisture, shade and slope exposure. The details of these garden plans are shown in figure 5.2. In studying the reaction of plants to transplantation into one or other of these habitats three measurements were deemed to be especially critical (cf. Clausen, Keck and Hiesey 1940: 57). These were: measurement of the longest stem (which gave a rough measurement of the plant's vigour), the number of flowering stems (which gave a rough indicator of the plant's reproductive vigour) and the date of appearance of the first flower (which indicated how quickly the plant had been able to come into season and hence its physiological tempo).

The results of these studies were broadly to confirm the insights which had been made in Turesson's work of the 1920's. The species which extended across considerable portions of the transect were found to consist of a series of climatic "races" or "ecotypes" each restricted to certain ecological zones on the transect, resulting in a series of more-or-less discontinuous ecotypes with (normally) characteristic morphology. And, in accounting for this variation, Clausen, Keck and Hiesey used the genecological terminology that had been developed by Turesson, applying this terminology in only a slightly modified way (see later). However, the cytological and genetical data which Clausen and his co-workers also gathered on each of the plant groups which they studied allowed a much fuller interpretation of the evolution and phylogeny in these groups to be built up than had been possible for the plants which Turesson studied. The nature of these results and the manner in which they were collated with the data gained from transplant studies is best illustrated by using some exemplars from Clausen's work.

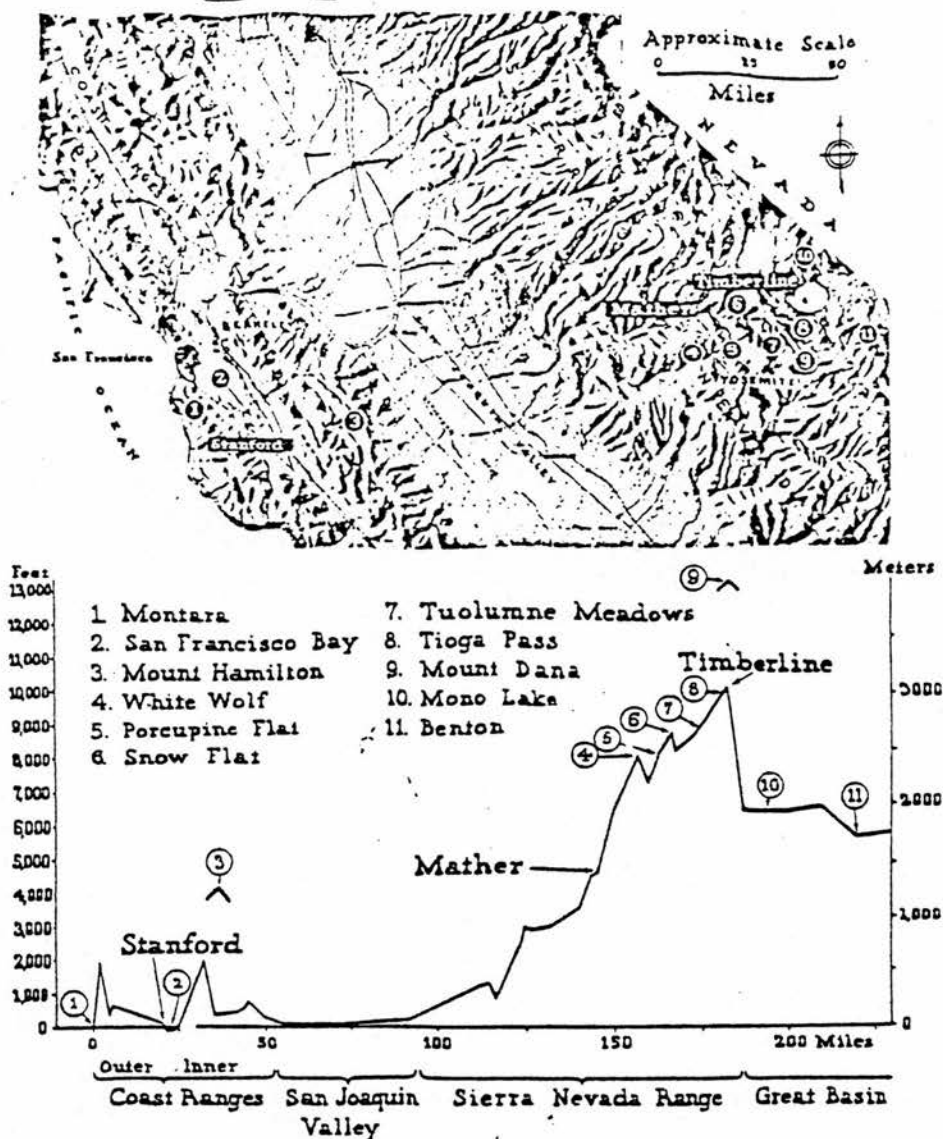


Figure 5.1. Relief Map and Profile of Central California (from Clausen Keck and Hiesey 1940:6).

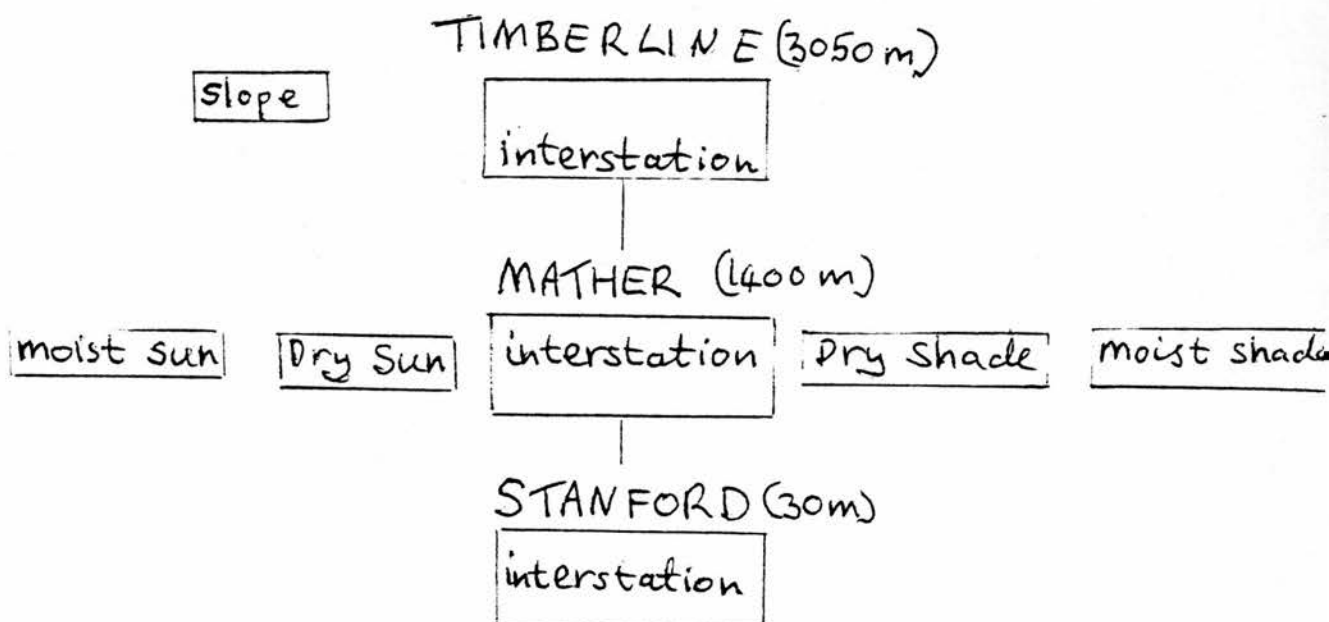


Figure 5.2. Plan of Gardens used by Clausen.

Example 1. Potentilla glandulosa and its allies (Clausen, Keck and Hiesey 1940: 25-124).

In Rydberg's (1908) analysis of this complex he had assigned the North American material into no less than 28 species. Clausen, Keck and Hiesey treated the North American material as composed of three species: P. arguta Pursh, P. fissa Nutt. and P. glandulosa Lindl. Transplant experiments showed that P. glandulosa in California could be subdivided into four regional ecotypes. One of these was a coastal race, previously recognised as P. glandulosa ssp. typica. Another, previously recognised as subspecies reflexa, was a mid-altitude ecotype found growing in the foothills of the Sierra Nevada mountains. The last two ecotypes, one sub-alpine and the other alpine had been lumped together in previous taxonomic treatments as P. glandulosa ssp. nevadensis. These four ecotypes were all distinguishable on the basis of external morphology, although the morphological differences were not sufficient, in Clausen's opinion, to warrant taxonomic recognition as separate species.

Cytological examinations revealed that all of these taxa were nearly identical in their chromosome morphology and that they all shared the same chromosome number ($n = 7$). Studies of hybrid populations where the geographical ranges of arguta, fissa and glandulosa overlapped showed that these groups could successfully exchange genes, although hybrid populations were, in fact, only rarely encountered. On the basis of this evidence Clausen, Keck and Hiesey were able to conclude that Potentilla glandulosa and its allies consisted of three ecospecies (glandulosa, fissa and arguta) which were themselves members of a single coenospecies (arguta) and which in turn could be divided into an indefinite number of ecotypes, of which at least four occurred in the Californian flora.

Example 2. The genus Zauschneria (Clausen, Keck and Hiesey 1940: 213-259).

North American species of Zauschneria had long been a problem group for taxonomists because of the apparent intergrading in certain areas of forms morphologically distinct elsewhere. Clausen, Keck and Hiesey recognised four species in this group: Z. cana Greene, Z. garrettii A. Nels., Z. septentrionalis Keck and Z. californica Presl. One of these,

Z. septentrionalis, was a previously underscribed species.

Transplant experiments revealed Z. cana, Z. garrettii and Z. septentrionalis to be monotypic, i.e. composed of a single ecotype. However, Z. californica, the most widespread and variable of the four species, was found to contain three ecotypes - all given subspecific status as Z. californica ssp. angustifolia, Z. californica ssp. latifolia, and Z. californica ssp. typica respectively.

Cytological data showed that Z. cana, Z. septentrionalis and Z. garrettii were all diploid ($2x = 30$). Z. californica, however, was tetraploid ($4x = 60$).

By means of crossing experiments Clausen and his group were able to demonstrate that exchange of genes between diploids and tetraploids was a rare but possible event (see figure 5.3). Crossing between the three subspecies of californica was relatively unproblematic, confirming their status as ecotypes of a single ecospecies.

The morphological, ecological, cytological and genetical data, when combined, also suggested a probable phylogenetic history of the group. Thus Z. californica angustifolia appeared to be an autotetraploid of Z. cana. Similarly, Z. californica latifolia appeared to be an autotetraploid derived by a doubling of the chromosome number of Z. septentrionalis. It also seemed likely that these two autotetraploids then hybridized to form the third tetraploid, Z. californica typica, which is intermediate between angustifolia and latifolia both with regards to its ecological habitat and morphology. This probable phylogenetic history of the group is shown in figure 5.4.

Clausen and his co-workers treated this group as comprised of a single coenospecies composed of four ecospecies and six ecotypes. This treatment, they felt, accorded best with the cytological and genetical data they had gathered, although from a phylogenetic point of view, it meant that Z. californica is a "polytypic" species, that is, it had originated from two separate tetraploid populations (themselves derived from separate diploid ancestors) which later became united by hybridization.

Example 3. Madia nutans (Clausen, Keck and Hiesey 1945: 4-6; Keck 1935).

Madia and Layia are two genera in the Compositae. M. nutans was

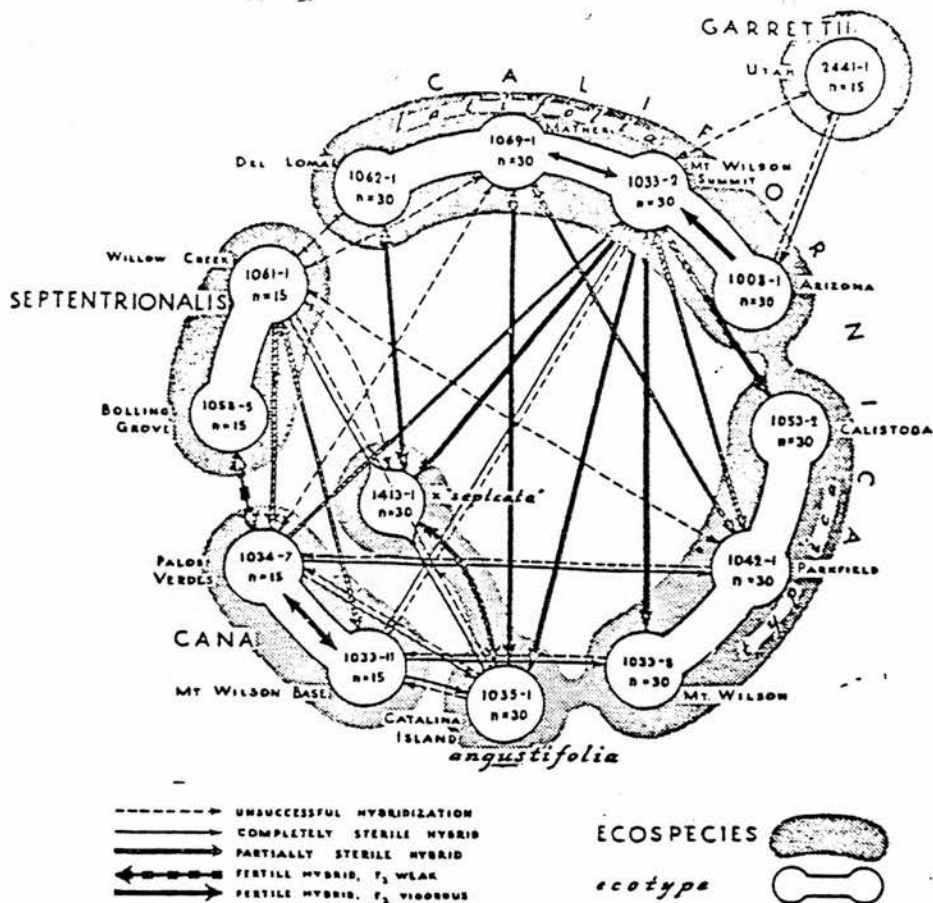


Figure 5.3. Crossing Experiments in *Zauschneria* (from Clausen, Keck and Hiesey 1940:248).

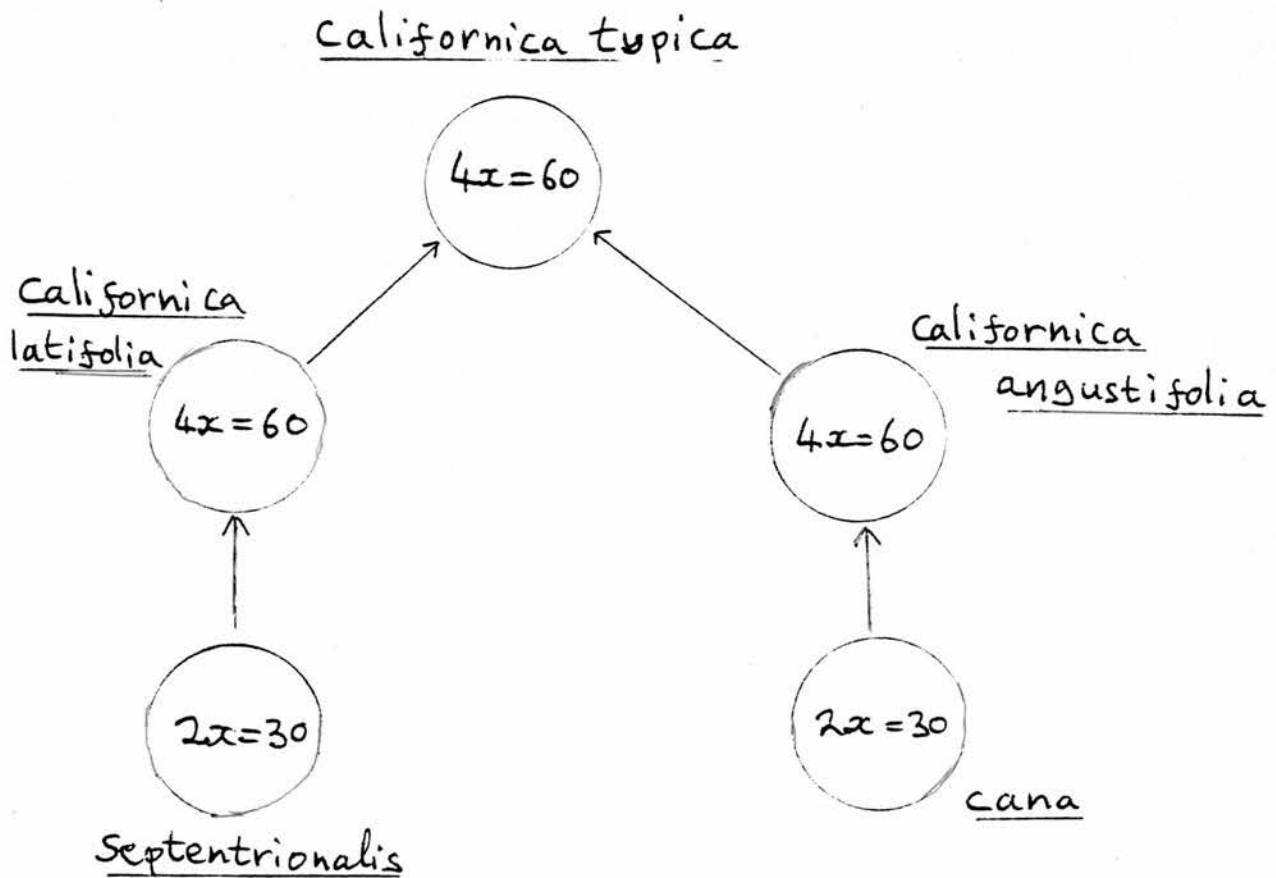


Figure 5.4. Phylogenetic Relationships in Californian Species of *Zauschneria*.

a species which all previous taxonomists had referred to the genus Layia. However, Clausen's group showed that nutans had nine pairs of chromosomes, a number not shared with the Layias which have $n = 7, 8$ or 16 , but a number which was found in one species of Madia (M. hallii). More importantly, crossing data showed nutans to be unable to exchange genes with any species of Layia, but that it could be crossed with at least five species of Madia. On the basis of this evidence Clausen and his colleagues decided that nutans was a member of the genus Madia, not, as had been the previous treatment based only on morphological considerations, a member of the genus Layia.⁸

With these examples in mind we can now reconsider the significance to experimental taxonomy and evolutionary theory of the work which Clausen and his co-workers were producing in the 1930's and 40's.

Three points deserve special attention. To begin with, as is evident from these examples, and indeed from the rest of Clausen's work, micro-evolutionary processes of speciation in angiosperms are exceedingly complex. Indeed, Clausen maintained that their complexity was far greater than could ever be discovered from simple laboratory experiments in genetics (Clausen, Keck and Hiesey 1942: 187). Hybridization, polyploidy, recombination, linkage, isolation, selection and mutation all operate in complex ways to bring about the existence of new species. The discovery of the role which polyploidy could play in plant speciation was an especially important element in the writings of Clausen's school, for, although the basic nature of polyploidy in plants had already been investigated some two decades earlier by Winge (see Winge 1917 and also Sturtevant 1966: 112-113), Clausen's group was the first to assimilate such data into the framework of experimental taxonomy. A second complexity revealed in Clausen's work was that most characters expressed in natural populations were not controlled by a single gene obeying strict Mendelian ratios. Rather, most characters investigated were clearly controlled by many genes at different loci and hence "polygenic". Thirdly, Clausen's work well illustrated the vast reserves of variation hidden in any local population of plants and manifested only in special habitats. Ecotypes, Clausen once maintained, are "nature's big banking

8. The main morphological character used to separate the genera Layia and Madia concerns the ray akenes which are of an intermediate shape in Madia nutans, providing further evidence for its questionable status.

account, its reservoir against possible disasters" (Clausen 1968: 423).

The second aspect of Clausen's work which emerges from the Potentilla, Zauschneria and Madia examples is their dependence on Turesson's concepts of the ecotype, ecospecies and coenospecies. With regard to the higher units of this hierarchy, Clausen, following the lead given in Turesson's later work, defined units in genetical terms (Clausen, Keck and Hiesey 1945: 62-69). Thus for Clausen two populations of plants which are only capable of a limited exchange of genes are members of different ecospecies. Populations entirely unable to exchange genes and produce fertile offspring with one another are members of different coenospecies. However, such groups may still be able to cross and produce sterile hybrids. Where even this is not possible the populations are members of a different comparium. Of ecotypes Clausen, again following Turesson, held that ecotypes within a given ecospecies are potentially capable of gene-exchange, although for physiological and ecological reasons they will often rarely do so in natural populations. Thus, Clausen, like Turesson, saw ecological variation within the species as discontinuous in nature; it is only at relatively rare points of contact between ecotypes that this discontinuity of form will be masked. And Clausen believed that the concept of linkage could provide a further explanation of why this discontinuous pattern of intraspecific variation was found in so many groups. In addition to physiological, geographical and ecological barriers, ecotypes differ so diversely genetically that hybrids between ecotypes will be often ill matched. This emphasis on the distinctiveness of intraspecific ecological groupings was to come under increasing attack after 1935.

Thirdly, although Clausen's group used Turesson's genecological system to describe their results, they did not see genecological categories as a replacement of the orthodox Linnaean system. Indeed, even although Clausen and his colleagues sometimes discovered cases where genetical and cytological data suggested a taxonomic revision, e.g. as in the case of "Layia" nutans, they were actually prone to defend where possible the value of a purely morphological classification:

It might be convenient and also correct to maintain a merely theoretical conception of species together with one for the practical taxonomy based upon easily observable and safe morphological characters.

(Clausen 1931: 303)

(F)or practical reasons two or more ecospecies that have no morphological characters to distinguish them may be treated as one taxonomic species.

(Clausen, Keck and Hiesey 1939: 106)

Further, Clausen and his co-workers also held to the view that the experimental classifications of plant taxa would be "usually found to correspond fairly closely to taxonomic units based on careful morphological and distributional studies" (Clausen, Keck and Hiesey 1945: 66-67).

Thus in their later writings Clausen's school expressed a view of experimental taxonomy and its relations to orthodox taxonomy which was wholly different to the views found in the earlier writings of Hall, Clements, Turesson and Cockayne. Experimental techniques and results were no longer seen as replacing those of orthodox taxonomy; instead the emphasis is on the need for mutual cooperation and synthesis. Cooperation and synthesis, rather than competition and replacement, are stressed in this new approach. The need to maintain a plurality of methods was linked to this research strategy:

Evidence of relationship should, therefore, not be sought along either morphological, ecological, genetical or cytological lines alone, but through the employment of all four criteria considered together.

(Clausen, Keck and Hiesey 1941: 167)

(A) system built one-sidedly on either genetics or cytology is just as unbalanced as one founded on morphology alone.

(Clausen 1949: 195)

A feature of this new approach based upon mutual cooperation between the two disciplines was that it required a rhetoric which did not devalue the skills and aims of traditional taxonomists. That Clausen was less critical of orthodox taxonomy than most other experimental taxonomists is clear from his own writings. The point also emerges in the writings of other members of Clausen's team, particularly the group's senior taxonomist, D.D. Keck. In 1959 Keck was asked to write a review article on the future of plant taxonomy for the journal Zoological Systematist. As one might expect of a man who for many years had been a colleague and co-author of Jens Clausen, Keck was enthusiastic about the future of experimental methods in taxonomy:

I have the feeling that the experimental methods will have a much greater impact on plant taxonomy in the next 50 years than they have had in the last 200.

(Keck 1959: 76)

But Keck was also careful not to devalue the need for non-experimental studies in plant taxonomy as well. The older herbarium taxonomy will continue to exist side-by-side with the new approach:

Biologically ... old mother earth has quite a few of her secrets left ... (W)e have not half finished our inventory of the kinds of life growing on her ... Just straight inventory work here, without the frills of a fancy methodology, is going to keep a lot of biologists busy for a long time.

(Keck 1959: 76-77)

The diverse methods employed by Clausen and Keck in their work resulted in a way of classifying species which is diametrically opposed to the way in which Putnam claims that scientists should (or do?) employ natural kind terms. According to Putnam the scientists seeks out hidden relationships, or essences, which then serve as the criteria for demarcating natural kinds, i.e. they act as "cross-world relationships". However, Clausen denied that any single property of a plant population, either in its morphology, chromosome number or genetic behaviour, could be employed in this fashion. In practice Clausen and Keck, wherever possible, used morphological features to demarcate plant species. But they did not do this because they believed that external morphology provided the most "essential" or "basic" properties of a species. Rather, their concerns were purely pragmatic and practical ones. In cases where phylogenetic, genetical and morphological markers lead to different "species" being found in nature then "the classification should preferably be practical" (Clausen, Keck and Hiesey: 1945: 43).

The use of many diverse properties of plants, cytological, genetical and morphological in demarcating species suggests that a model of classification like Searle's "cluster theory model" might be applicable in this instance. However, again it can be seen that this is not the case. Clausen and Keck did not give equal weighting to cytological, genetical and morphological data in producing their classifications. Rather they weighted some properties more than others. Whenever possible genetical data was given the greatest weighting, e.g. as in the Madia

nutans example discussed above. However, where genetical evidence conflicted very strongly with morphological treatment, i.e. where a genetical demarcation of the group would make the two "species" concerned impossible to identify in the herbarium by means of morphological markers alone, then it was morphological characters which determined the final classification adopted. But, and this is the important point, in both cases the decisions which were made reflected practical concerns and instrumental interests. Concerns of this nature have to be understood by examining the usage of predicate terms in the practical contexts in which such predicates are used and developed. Logic alone, either of the Putnam "hidden essence" kind or the Searlian "descriptive association" kind is not a reliable guide to predicate usage. Language (and, by implication, knowledge) is a social phenomenon and its development cannot be captured in the abstract principles of symbolic logic or in the all pervading influences of some mysterious "hidden reality" which lies somehow beyond and outside the boundaries of human interests and cognition. Any model of classification which does not take into account the conventional and pragmatic nature of systems of classification is doomed to failure, if it is claimed to be naturalistic account of the actual nature of classification.

Other American Schools of Biosystematics, 1930-1950

Although not engaged directly in transplanting experiments or genecology, there were a number of other research schools in the U.S. in the 1930's and 40's which were actively involved in research that could be termed "biosystematic". Most of these researches were concerned with studies in genetics and cytology in their own right, but also yielded data which was of significance for the taxonomy of the groups being studied.

A good illustration of this kind of work was the detailed investigations, carried out over a number of years, on the genus Crepis (Compositae) by E.B. Babcock and his associates at Berkeley. Ernest Brown Babcock was, from 1913 to 1947 a professor of genetics at the University of California at Berkeley and a leading figure in the American genetics community. His associates included a number of prominent cytologists and geneticists, of whom the most notable was George Ledyard Stebbins (1906-), who succeeded Babcock as professor

of genetics when he retired in 1947.

The work on Crepis was begun in 1919 with the intention of carrying out an "investigation of fundamental genetical principles through breeding experiments, cytological work and taxonomic studies on various species of the genus" (Babcock, R.E. Clausen, Collins and Mann 1922: 3). In fact, it was hoped at this stage to use these plants to repeat the insights which had been gained into genetic mechanisms in Drosophila by T.H. Morgan and his Columbia school (Babcock 1920: 270). Crepis was considered an ideal genus for this kind of study. It is a large taxon (there are about 196 species in the U.S.), with a short life-cycle and, most importantly of all, few and large chromosomes which can be easily stained, counted and studied. The results of over twenty years of research on this genus was published in a number of separate papers (Babcock and Navashin 1930; Babcock and Stebbins 1937; Babcock and Stebbins 1937; Babcock 1942, 1944), and in a two-part monograph (Babcock 1947). Two aspects of this research may be considered separately: its significance from the standpoint of genetics and evolution, and its significance for experimental taxonomy or biosystematics.

The evolutionary picture which emerged of the genus Crepis was one which confirmed in its broad outlines the research being done both by Morgan's school at Columbia and Clausen's researchers at Stanford. Adaptation through gene mutation and the action of natural selection was found to be the major process of evolution at work in this group (Babcock 1944). Polyploidy was rare in this genus but, from a combination of cytological and taxonomical studies, Babcock and his associates were able to show that evolution in Crepis was linked with a progressive decrease in chromosome numbers. The most primitive members of the genus have a chromosome number of $n = 12$, the most advanced $n = 6$, with $n = 8$ and $n = 10$ as intermediate numbers. Further, the relatively small number of chromosomes involved and their large size allowed changes in chromosome number and morphology to be studied in detail.

There was considerable contact between the Stanford and Berkeley groups. Clausen, while still in Copenhagen, had spent a summer in Berkeley working on Crepis cytogenetics. The product of that research was a joint paper with Babcock (Babcock and Clausen 1929) concerned with

irregularities of meiotic division in hybrids and species of the genus. In addition, Babcock, in a letter to Göte Turesson written in 1935, mentioned monthly meetings between the Stanford and Berkeley groups.⁹ When the monograph on Crepis was finally published in 1947, it was Jens Clausen who provided a generally enthusiastic review of the work in the newly established journal Evolution (Clausen 1949).

In their taxonomic treatment of the genus Babcock and his co-workers made an attempt to synthesise the old and new taxonomy. For Babcock (1947: i, 31) a "truly scientific taxonomy" must rest upon the "broadest possible foundation". In their work on Crepis Babcock's group made some drastic revisions to the then current taxonomic conceptions about the genus, including the expulsion of some of the species to a separate genus Youngia (see Babcock and Stebbins 1937). However, following orthodox taxonomic practice, Babcock and his co-workers insisted that comparative morphology must continue to provide the bulk of the evidence used for systematic treatment and revision. Experimental evidence could suggest where morphological discontinuity might be looked for, and, wherever possible, the taxonomic treatment of the group was made to coincide with genetical and evolutionary knowledge about the species concerned. But, where experimental and morphological data were contradictory, then it was the latter which were used to provide the evidence on which the group's classification was made. Clausen felt that Babcock went too far in this direction and undervalued the significance for classification of experimental data. In his review of the monograph on Crepis he argued that Babcock's experimental work had influenced his treatment of the group's taxonomy to a greater extent than had been claimed (Clausen 1949: 186).

A second important figure in American genetical taxonomic research during the 1930's was Edgar Anderson (1896-), a botanist at the Missouri Botanical Garden, St. Louis. During the late 20's and 30's Anderson published a number of short monographs on Tradescantia (Anderson and Sax 1936; Anderson 1936a), Apocynum (Anderson 1936b), and Iris (Anderson 1928, 1936c). The aim of these studies was to examine the genera concerned "from the diverse viewpoints of genetics, taxonomy

9. E.B. Babcock M.S., letter (9 December 1935, Turesson archives, Lund University library.

cytology and biometry", and in this way to shed light on the general problem of what constitutes a species and its manner of evolution (Anderson 1936c: 457). A distinctive feature of Anderson's work was his interest in mathematical and statistical studies of variation. He was responsible, with the English botanist W.B. Turrill, for efforts to persuade herbarium workers to collect specimens in such a way as to permit biometrical studies on the samples.¹⁰ However, Anderson's major contribution to biosystematical studies and techniques was his work on hybrid indexes and his discovery of the phenomenon of introgression (Anderson and Hubrich 1938; Anderson 1949, 1953).

Introgressive hybridization (or introgression) is the gradual infiltration of genes from one species into another. It occurs when hybrids of two different species back-cross over a number of generations into one or other of the parental species populations. This process is illustrated in figure 5.5. Its significance in evolutionary terms is that it increases the variability of populations and leads to the formation of new gene combinations upon which selection can operate. The result is a hybrid swarm, i.e. a population of plants with high variability ranging from, on one extreme, plants which are typical or nearly typical of pure populations of one of the parental species to plants, on the other extreme, which are typical or nearly typical of the second parent. In between will be all shades of intermediate forms whose nature will be determined by the degree of introgression which has taken place.

The hybrid index was an analytical tool devised to deal with such hybrid swarms. By this technique characters typical of one parent were scored as 0, characters typical of the other parent scored as 2, and intermediate characters scored as 1. The result when a hybrid swarm is analysed in this fashion is a frequency distribution on which the hybrids given low scores represent pure or nearly pure members of one parental species and hybrids with high scores represent comparatively pure individuals of the second parent (see figure 5.6). Such hybrid

10. The idea put forward was that herbarium taxonomists should collect sizeable numbers of parts of a plant, all specimens being taken from a single local population. This would allow biometrical studies of the material (Anderson and Turrill 1935; Anderson 1941).

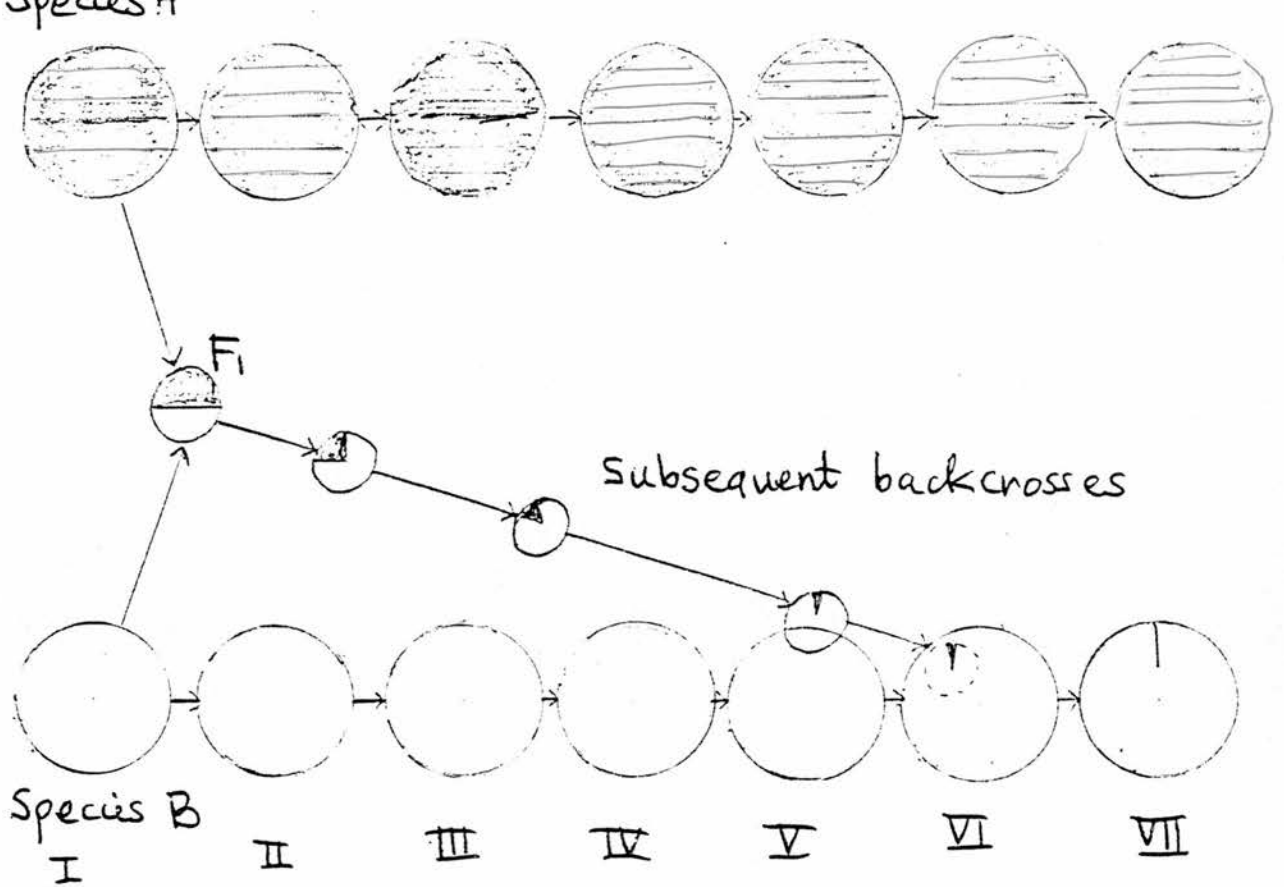
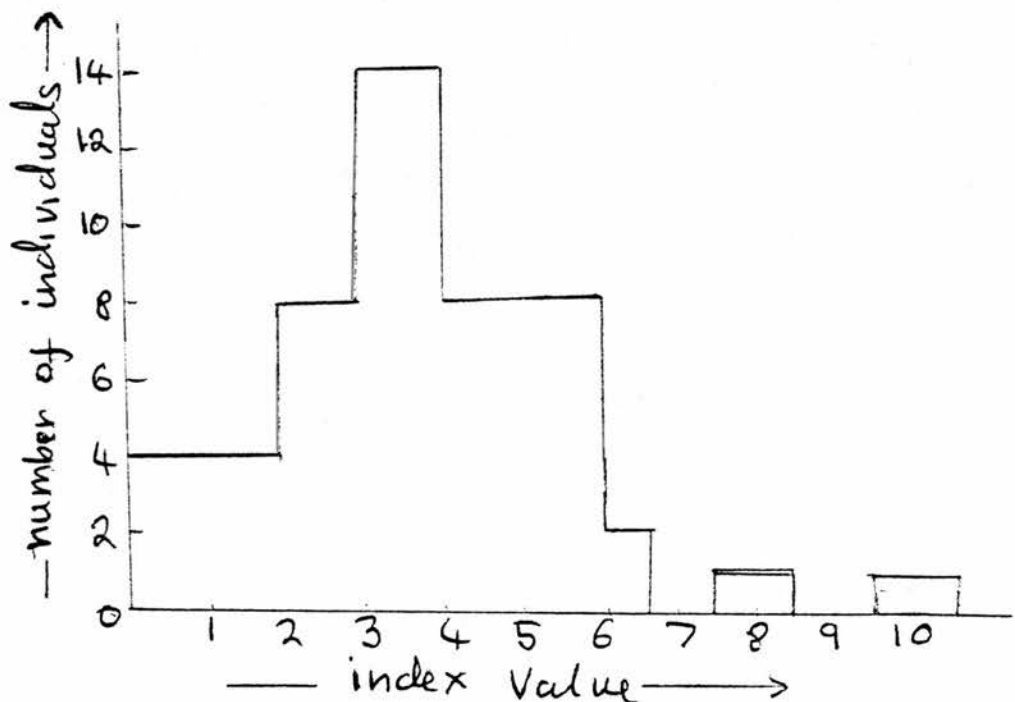


Figure 5.5. Diagram illustrating Introgression
(from Davis and Heywood 1943:466).

Figure 5.6. Frequency Distribution of 50 Plants on a
hybrid index with values of 0 for pure *Oxytropis*
albiflora and of 12 for the opposite extreme
(from Anderson 1953:287).



indexes, together with pictorial scatter diagrams, were the major techniques Anderson employed to study introgression.¹¹

The whole question of hybridization in evolution had great significance for taxonomists because it re-opened the problematic question of how hybrids should be treated for taxonomic purposes. The passion with which this topic was debated is well shown by the fierce controversy which raged in the journal Chronica Botanica between 1939 and 1941.¹²

The starting point of this controversy was an article by the Dutch taxonomist H. Uittien (1939) entitled "Reflections on the Nomenclature of so-called Hybrids". Uittien's proposals were two-fold; firstly, that hybrids should not receive taxonomic recognition and secondly, that it was undesirable that genetical and cytological data should be introduced into taxonomy. Uittien's view was that taxonomy should be concerned not with evolution but with the products of evolution, and that it should be based upon morphology and not parentage. The taxonomist is concerned with the characters of plants, not with their origin.

Uittien's position was strongly criticised by the American taxonomist F.R. Fosberg (1939). In his reply to Uittien, Fosberg claimed that hybrids must receive taxonomic recognition and that to exclude phylogenetic considerations from taxonomy is to render impossible the achievement of a genuinely natural system of classification. Fosberg ended his critique of Uittien's paper by comparing the latter's position to that of "a well-known American taxonomist of the last century" who had not accepted the doctrine of evolution and who, when confronted with intermediate forms, consigned them to the dustbin on the grounds that they represented the work of the devil (Fosberg 1939: 398).

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11. For an account of pictorial scatter diagrams and their role in detecting hybrid swarms see Davis and Heywood (1963: 476-479)
 12. It is interesting that the major protagonists in this debate were all taxonomists by profession rather than geneticists or cytologists. H. Uittien and C.E.B. Bremekamp were both herbarium taxonomists at Utrecht; F.R. Fosberg was a taxonomist at the University of Pennsylvania; W.B. Turrill and J.S.L. Gilmour were both at Kew Gardens, Richmond, Surrey.

However, Uittien's remarks received enthusiastic support from another Dutch botanist, C.E.B. Bremekamp (1939). Bremekamp argued that hybrids should only be named if they are morphologically distinct from their parents and if they breed true to form in subsequent generations. Also, if this is the case, Bremekamp maintained that these "hybrids" should be given normal binomial names just as would any other species. Like Uittien, Bremekamp was sceptical of the role which genetics could or should play in taxonomy:

For the moment the attitude of the taxonomist towards the progress of genetic investigations should be that of an interested spectator, not more. If he engages himself in hybridization experiments, he should know that he leaves the domain of taxonomy.

(Bremekamp 1939: 403)

Fosberg's reply (1941) to Bremekamp was even more polemical than his original article attacking Uittien. In it he accused Bremekamp of trying to "seal off" taxonomy from the new approaches of genetics, evolution and phylogeny, and he described such an exercise (p. 396) as both "futile" and a "folly". He also claimed, on the basis of a personal survey conducted amongst American taxonomists, that the majority of them (about 75%) did not agree with the opinions of Uittien and Bremekamp. He ended his article with the conclusion that:

My conception of taxonomy is that of a growing, dynamic science, making use of new information and methods as fast as they appear, not that of a hide-bound unprogressive, static discipline such as is usually referred to as 'closet' botany.

(Fosberg 1941: 370)

By 1941 the two British botanists J.S.L. Gilmour and W.B. Turrill had joined the debate. In an apparent attempt to pour oil on troubled waters Gilmour and Turrill (1941) suggested that, while Bremekamp was right in rejecting phylogeny as the basis for taxonomy, a classification based upon overall resemblances must use information drawn from as many sources as possible, including genetics and cytology. This position conflicted with the views expressed by both major protagonists in the controversy. In his reply to Gilmour and Turrill, Bremekamp (1942) repeated Uittien's earlier claim that taxonomy must deal with the products of evolution and not with data concerning the hypothetical origin of such units. Fosberg, in his comments on Gilmour and Turrill's paper,

repeated his claim that for a classification to be worthwhile it must reflect evolutionary descent. Thus, when the controversy ended in 1942, no position of agreement had been reached.

The final American taxonomist whose work will be discussed in this section is W.H. Camp. During the 1940's Camp was a botanist at the New York Botanical Garden. Originally trained as an orthodox taxonomist, Camp became an enthusiastic advocate of the new taxonomy and was the first biosystematist to become a President of the American Association of Plant Taxonomists. Indeed, it was Camp and his student C.L. Gilly who first used the term "biosystematy", later altered to become "biosystematics" (Camp and Gilly 1943). As initially conceived of by Camp and Gilly the objectives of biosystematy were "1. the delimitation of natural biotic units and 2. the application of these units to, a system of nomenclature adequate to the task of conveying precise information regarding their defined limits, relationships, variability and dynamic structure" (Camp and Gilly 1943: 323). Thus the objectives of biosystematy were roughly the same as those of experimental taxonomy as defined by Hall and Clements and later by Clausen, Keck and Hiesey.

The central feature of Camp's writings in biosystematics was the claim that the term "species" as utilised by classical taxonomy lacked any precise operation definition. In order to prove this point Camp (1951) asked three herbarium taxonomists to classify the same set of herbarium samples into their component species.¹³ The plant genus chosen for this "experiment" was North American material of the genus Rubus (blackberry), a group in which it is notoriously difficult to delineate species because its reproduction is partially apomictic. In dealing with this material, one taxonomist said that there were 381 species, one said that there were 205 species and one taxonomist divided the material into just 24 species. Commenting on these results, Camp posed the question:

Do these three leading exponents of classical taxonomy not know what a species is ... Or is it that classical taxonomy lacks precise definitions of its terms?

(Camp 1951: 118)

13. The taxonomists were L.H. Bailey, M.L. Fernald and H.A. Gleason.

And he concluded that:

The naked truth is that the basic working unit of classical, empiric taxonomy - 'the species' - is not, and never was, defined with sufficient biological soundness and precision to be called a science. It is an art.

(Camp 1951: 118)

Camp's solution to the "species problem" was that the term "species" should be abandoned altogether. In orthodox taxonomy he recommended that the term should be replaced by the concept of the "binom", the latter being "a tentatively defined taxon, consisting of one or more specimens in a museum collection to which a binomial has been attached, but of whose biogenic pattern we have no experimental information" (Camp 1951: 120). In ^Sbio_^systematics the term species should be replaced by a whole battery of concepts designed to illuminate, from a genetical and evolutionary perspective, the different kinds of plant populations which were formerly referred to as species. (This positive aspect of Camp and Gilly's work is looked at in more detail in a later section of this chapter).

Underlying this attempt at nomenclature reform was the desire to modernise taxonomy and make its system of classification relevant to the needs of geneticists, cytologists and students of evolution. As Camp forcefully stated in an earlier paper:

The day of the taxonomist who putters alone in his herbarium with an other-worldly state is done. He must shed off his robe of academic classicism and seclusion, brush off the accumulated dust of the centuries, and come face to face with the dynamics of living populations.

(Camp 1943: 342-343)

The idea that plant classifications could and should reflect evolutionary, genetical and cytological knowledge about the taxa concerned was thus a prevalent notion in the writings of experimental taxonomists in the 1930's. However, by 1935 evidence was beginning to accumulate within genecology which suggested that intraspecific variation was not of a kind which was amenable to systems of classification either of the orthodox or of the biosystematical and genecological kind. The chief exponents of this new approach within genecology were a group of Scottish botanists led by James Wylie Gregor (1900-). It is the work of Gregor and this Scottish school of genecology that we shall examine next.

James W. Gregor and the Scottish School of Genecology

James W. Gregor was born at Innerwick, Midlothian in 1900. Educated at the University of Edinburgh from which he obtained a Ph.D. in 1926, Gregor went on to become chief assistant (1926-1949) and later Director (1950-1965) of the Scottish Plant Breeding Station at Corstorphine, near Edinburgh.

Gregor had read the first of Turesson's papers in Hereditas and his interest in genecology stemmed from this. The doctoral dissertation (Gregor 1926), although primarily concerned with a study of the genetics of agricultural grasses with the aim of finding improved techniques in their breeding, incorporated a genecological perspective in its theoretical orientation.

Gregor's earliest papers on genecology also concerned Gramineous plants (Gregor and Sansome 1927, 1930; Gregor 1931). Much of this early research was done in conjunction with the cytologist F.W. Sansome, a student at the Plant Breeding Station who later moved to Glasgow University and then to the John Innes Horticultural Institute at Merton in London. The aims of these early papers were, as the authors put it, "to elucidate the connection between genetics and ecology, a connection which until recently has not been made prominent" (Gregor and Sansome 1927: 349). By using the techniques of transplant analysis Gregor and Sansome were able to show that there existed definite habitat types within the species of the grasses being studied and that the variation between them was inherited. In applying a classificatory scheme to these findings Gregor employed the ecotype-ecospecies terminology of Turesson who was praised for bringing into being "a constructive attempt to place the groupings of organisms on a more natural basis" (Gregor 1931: 206). Indeed, Gregor's 1931 paper adds to the genecological terminology a new concept - the "geo-ecotype" - used to denote units of ecotypic status, the distinctive characters of which have arisen by chance geographical isolation, rather than under the forces of natural selection.

However, it was not the studies on grasses which were to prove the most important work of Gregor and his colleagues. In the late 1920's Gregor had also begun similar studies on the sea plantain (Plantago maritima L.). Plantago maritima proved an excellent species

for study, with a circumpolar distribution, wide intraspecific variation and easily measurable growth characteristics. In a series of classical papers on the experimental taxonomy of this species published between 1930 and 1942 Gregor and his co-workers set out to substantially alter the trends which had been prevalent in genecological research during the previous decade. The methods used to study P. maritima were the by now familiar ones - a combination of cytological research, studies of fertility and experimental transplants (Gregor, Davey and Lang 1936: 326). However, the results obtained indicated a significant departure from those obtained in previous genecological studies.

The first indication of the unusual data being obtained on Plantago was contained in the 1936 paper where the authors reported that "in sea-plantains discontinuous variations are few and have little importance ... Many quantitative characters ... vary continuously within the populations" (Gregor, Davey and Lang 1936: 347). However, the decisive break came in a 1939 paper, with Gregor as the sole named author, which summarised the results of the previous nine years of research on European and North American material of Plantago maritima. The starting point of Gregor's argument was that experimental taxonomists must evolve their own systems of classification rather than employ the existing morphological system:

Until more is known of the specific and infra-specific categories of variation in the wild, a too precipitate amalgamation of experimental and traditional taxonomy would almost inevitably have repercussions detrimental to the present usefulness of the established morphological system. Therefore, in the meantime, it would seem more appropriate for experimental taxonomists to refrain from attempting to meet their requirements by any redefinition of the orthodox classificatory categories, but instead to use a complementary system of classification with a distinctive terminology, at least until the true value of the new categories, and their possible place in a more comprehensive system can be assessed.

(Gregor 1939: 294)

The question became: what sort of terminology should experimental taxonomists adopt? Gregor argued that the Turessonian terms "coenospecies" and "ecospecies" should be retained, but he also argued for the need to create new terms to replace the ecophene and ecotype. To describe a population in terms of morphological discontinuities implies that such combinations (i.e. ecotypes) are static and morphologically stable. But, using the data obtained on P. maritima

Gregor argued that few populations within this species are morphologically stable in this manner. Thus, emphasis must be shifted from describing populations in terms of discontinuities in character complexes to the recording of populations typifying particular kinds of variation, regardless of the degree of aggregate morphological distinctiveness involved. To this end Gregor proposed a new infra-specific terminology centred around the concept of the "cline" and with categories defined as follows:

- cline: any gradation in measurable characters;
- topocline: a cline following a geographical gradient;
- ecocline: a cline apparently correlated with an observable ecological gradient;
- topotype: a population in a geographical region possessing characters differing from those of another region. A topotype may be extraclinal if it does not fall within a geographical gradient in character expression, or intraclinal if it has reference to a particular range on a geographical gradient;
- ecotype: a particular range on an ecocline;
- microtopotype: a micro-geographical population, primarily the result of a chance fractionation of a parent population;
- exotype: a hereditary aberration which occurs so rarely and so sporadically, that it never becomes a feature of any population: the category of exotype is, therefore, not a population concept.

(Gregor 1939: 321-222)

The most important property of the cline terminology is that it can be used to describe intraspecific variation in terms of continuous characters rather than discontinuous types. The ecotype, where it occurs at all, becomes a range on an ecocline. Gregor was not the first botanist to suspect that intraspecific variation might be -- continuous in form. The Swedish physiological ecologist Otto Langlet had suggested in an autecological study of the genus Pinus made in 1934 that, since most major habitat factors vary spatially in a continuous and not a stepped manner, graded rather than discontinuous variation might be expected in wide-ranging species as a consequence of adaptation to the habitat (see Langlet 1934, 1936 and Faegri 1937a). Nor indeed was the clinal concept itself original, since Gregor had borrowed the term from Julian Huxley's work on animal populations (Huxley 1938).¹⁴ However, Gregor

14. This is of interest because it represents one of the few substantial links between the growth of animal and plant biosystematics.

was the first genecologist to advise a full nomenclatural system from this work and set it up in opposition to the established ecotype hierarchy - a move which inevitably highlighted the differences between the two approaches to intraspecific variation and its taxonomic treatment.

As indicated above, the change to a model of continuous variation for dealing with taxa below the level of the species necessitated a rethinking of the boundaries between genecology and orthodox taxonomy. In his 1944 review of the ecotype concept Gregor recommended that ecological variation within species should only be given taxonomic recognition where the populations concerned possessed very clear and definable morphological markers. He suggested the term "ecoclinal subspecies" to cover such cases. Where, as in the more common case, variation is clinal and can only be subjectively defined, formal taxonomic names should not be given (Gregor 1944: 29). Indeed for Gregor the urge of genecologists to classify ecological variation was becoming a hindrance rather than a help. The object of genecology should be to study the processes of speciation, and Gregor, unlike Hall, Clements, Turesson and Clausen, came to see this aim as an objective incompatible with that of classification. Thus, in a 1946 paper on genecology and its relation to classification we find Gregor arguing for the separation of these two objectives:

In conclusion it is tempting to suggest that instead of trying to define all intra-specific variation in terms of traditional taxonomy, a more detailed picture of the internal structure of species would be obtained by freely admitting that the classification of ecotypic variation is a special purpose one involving its own peculiar concepts and techniques. The need at the moment is to overcome the almost subconscious desire to resolve intra-specific variation into categories capable of being absorbed into the orthodox taxonomic system, and the current emphasis on the discontinuities in the distribution of ecotypic variation, rather than on ecotypic trends, is perhaps only a reflection of this taxonomic undercurrent.

(Gregor 1946a: 389-390)

And this passage is immediately followed by one in which Gregor defended orthodox taxonomic practice and the general-purpose classifications thereby produced.

The desire to keep micro-evolutionary units separate from those employed in orthodox taxonomy is also evident in the second genecological

nomenclature produced by Gregor - the "deme" terminology founded in collaboration with J.S.L. Gilmour (Gilmour and Gregor 1939), and later modified by Gilmour and Heslop-Harrison (1954) and Gilmour (1958).¹⁵ The units of formal taxonomy were rigidly excluded from this system, even as prefixes or suffixes in compound terms. The basis of this terminology was the "deme", defined simply as, "an assemblage of taxonomically closely related individuals" (Gilmour and Gregor 1939: 333). To this term there could be added appropriate prefixes as more information was gained about the populations under study. Thus, for example, we can have:

<u>gamodemes</u> :	demes forming more or less isolated local breeding communities;
<u>topodemes</u> :	demes occupying a specified geographical area;
<u>ecodemes</u> :	demes occupying a specific ecological habitat. ¹⁶

The deme terminology was meant as a "neutral" system of concepts to be applied in cases where little evidence had been accumulated about the populations of plants under study. It was not intended to replace either the ecotype or ecocline systems, although the term "ecodeme" was supposed to be used in situations where insufficient data had been gathered to make application of either of these terms feasible. Similarly, it was not intended to replace the morphological species, subspecies, and varieties of the herbarium taxonomist (Gilmour and Gregor 1939: 333). The chief advantage of the system was its flexibility. However, in practice, the system was little used and, where it has been employed, this has been in a manner inconsistent with the original intentions of its creators (Gregor, personal communication, 1 July 1977).

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15. In these later publications Gilmour advocated the deme terminology as a system which could be used by evolutionary taxonomists without recourse to the term 'species' even in the peripheral sense of Turesson's ecospecies and coenospecies. In effect, Gilmour's suggestion was that the best strategy for evolutionary taxonomists was to abandon altogether any attempt to revise the orthodox categories of taxonomy and instead provide "special-purpose" classifications of their own.
16. These were the three examples given in the original 1939 paper. Others have been added since, most notably the cytodeme - used to denote chromosomal races within the Linnaean species.

In summary, it can be said that, while the work of Gregor and his associates had its origins in the genecological studies of Göte Turesson, their findings, especially after 1935, reveal a growing movement away from Turesson's original position. While Turesson and Clausen maintained that ecological variation within the Linnaean species was discontinuous in form, Gregor came to view such variation as normal clinal. For Turesson populations which occupied a distinct habitat represented an objective, territorial ecotype. For Gregor the ecotype was to be defined subjectively, as an assemblage of more or less separate breeding communities lying along gradients of climatic, edaphic, or biotic factors. Finally, Turesson had held that genecological classifications would replace the Linnaean system used in orthodox taxonomy. In Gregor's work genecological systems represented "special-purpose" classifications intended to supplement and not to replace the normal approach, and the task of constructing such classifications was only given a minor role: the prime task of genecology was to be the study of evolutionary processes, a task not always compatible with that of classification.

Gregor was not the only botanist who worked on Plantago from a genecological perspective. The Danish phytogeographer and cytologist Tyge Böcher (1909-) working at the University of Copenhagen carried out, between 1939 and 1941, cytological, taxonomical and transplant studies on the Danish populations of Plantago lanceolata L. Böcher (1943) was able to confirm that ecological variation in this species of Plantago was also clinal and not discontinuous. Since, in his earlier papers on genecological studies of Campanula rotundifolia (Böcher 1936) and Brunella vulgaris (Böcher 1940), he had employed Turesson's ecotype terminology, Böcher's conversion to the ecoclinical concepts of Gregor represented a further advance of the Scottish school's position. The questions raised by the work of Gregor and Böcher as to whether ecological variation is primarily continuous or discontinuous and the extent to which genecologists should be concerned with classifying such variation, have remained central themes in the genecological literature up to the present day.

The work of Gregor and his associates is, like the work of Clausen's school, hard to reconcile in terms of Putnam's account of scientists as people who go out and classify the world in terms of hidden essences. In his later work Gregor came increasingly to see classification of

intraspecific units in any terms as something which might hinder rather than help in understanding evolutionary processes and relationships:

(W)hen a graded series of forms exists naming them does nothing to bring out the connections between the forms and it may, indeed, even serve to disguise such relationships.

(Gregor 1946b: 268)

Gregor's argument was not one designed to show that scientists should cease the activity of classification altogether. But Gregor did realise that any system of classification by its very nature involves emphasising some relationships more than others, and any classification involves obscuring some relationships as well as highlighting others. The value of a classification lies in the usages to which it is put. No system of classification can be said to be more "real" or more "perfect" than any other in some final and transcendent sense. All systems of classification can be evaluated only in the context of the purposes to which they are designed to serve. In recognising that genecological classifications, and indeed morphological classifications as well, were of the nature of "special-purpose" classifications, Gregor and his associates did more than just suggest a new avenue of research for genecology; they made a point of fundamental importance to the understanding of all systems of classification.

Other British Biosystematists, 1930-1950

While James Gregor was undoubtedly the most prominent figure in British genecology during this period, there were a number of other British botanists concerned with the interface between plant genetics and taxonomy of whom the most important were W.B. Turrill, E.M. Marsden-Jones, J. Heslop-Harrison, D.H. Valentine and J.S.L. Gilmour. Of these figures W.B. Turrill (1890-1961) is of particular interest in that he was one of the most influential herbarium taxonomists in Britain and a highly respected figure in the orthodox taxonomic community, being assistant keeper (1909-1946) and later keeper (1946-1957) of the herbarium at Kew. Turrill's main research output concerned floral and phytogeographical studies of the Balkan Peninsula, but in collaboration with the cytologist E.M. Marsden-Jones (1890-1960), he also published a considerable amount of research on the genetics and ecology of Silene, Centaurea, Ranunculus, Anthyllis and Saxifraga.

In his writings Turrill was careful to stress the value of orthodox taxonomic research, which he labelled "alpha" taxonomy, in contrast to the "omega" taxonomy which becomes possible when a group's full ecology, genetics and cytology is known. Like Gregor, Turrill saw the ecotype system as a special-purpose classification, which did not serve as a replacement for the existing morphological system:

It is hardly necessary to remind readers of the great achievements of alpha taxonomy ... Further, probably only a taxonomist working in one of the large museums or herbaria can realise how much still remains to be done by the established taxonomic methods.

(Turrill 1938a: 33)

And Turrill was particularly critical of those experimentalists who wanted to define species in terms of genetic criteria without regard to morphological relationship:

There has been an increasing tendency in theory to emphasise sterility-fertility criteria ... The taxonomist cannot help objecting to the overwhelming importance that is given to sterility-fertility criteria at the ecospecies level.

(Turrill 1946: 39-40)

However, these criticisms were not levelled at experimentalists because Turrill wanted to seal off herbarium taxonomy from the new approaches. On the contrary, Turrill was concerned that efforts should be made to incorporate the new kinds of methods into "alpha" taxonomy whenever this was practically possible. It was one of Turrill's maxims that an experimental garden and laboratory should be attached to every herbarium and vice versa (Turrill 1925: 360; Marsden-Jones, Summerhayes and Turrill 1930). In his forward to Heslop-Harrison's (1953) textbook on experimental taxonomy, Turrill talked of the need for an introgressive hybridization of methods and ideas, the result of which will be "hybrid vigour" in taxonomy. The same objective is also evident in a joint letter to Nature, written with E.S. Anderson, urging that herbarium workers should begin to collect specimens in such a way as to permit biometrical analysis of the plant material which was being assembled (Anderson and Turrill 1935; and see also Anderson 1941).

The work of Turrill, with its emphasis on the need for mutual cooperation between taxonomists, geneticists, cytologists and ecologists,

has many parallels with the position adopted in Clausen's research. Emphasis again is placed on the value of diverse methods combined into a synthetic approach to the problems of classification. Indeed, Turrill was an enthusiastic advocate of Clausen's work, which he saw as a positive attempt to correlate genecological nomenclature and practice with orthodox taxonomic methods and aims (Turrill 1939). However, Turrill's belief that a synthesis was possible between genecology and orthodox taxonomy was at variance with James Gregor's genecological theories (Gregor, personal communication, 1 July 1977). In fact, the prevailing trend in genecology since 1950 has been one involving a separate development from orthodox systematics, a trend which in his later years Turrill tried very hard to reverse (see, for example, Turrill 1958).

Genecology in Russia

An important school of genecological studies developed in Russia under the direction of Eugenija Nikolaevna Sinskaya (1899-1965). Sinskaya was an external student from 1909 to 1917 at the Petrov Academy of Agricultural Science in what is now Leningrad. After completing her degree she was, from 1919 to 1921, an assistant to the great Russian plant breeder N.I. Vavilov, and she moved with Vavilov to join the staff at the Bureau of Applied Botany, later re-named the All Union Institute of Plant Industry, Leningrad. Apart from three years of exile during World War II, Sinskaya remained in Leningrad until her death in 1965. Her work at the Leningrad Institute produced a voluminous literature on the genetics, ecology, taxonomy and breeding systems of higher plants, many of these studies being conducted on crops of agricultural importance in the Cruciferae.¹⁷

The genecological research of Sinskaya and her associates can be divided into two periods. The first of these, which involved pre-War investigations, was concerned with ecotype recognition and classification in wild populations. This result of this phase of the research was published in Sinskaya's book Dynamics of Species (1948). Post-War investigations were more concerned with studies of plants of agricultural significance. A summary, in English, of this later phase of research is given in Sinskaya (1958).

17. Most of this work has never been published in English. However, a complete list of the English translated titles of her works was published together with an obituary notice in taxon. See Bakhteyev, Lizgunova, Mordvinkina, Suvorov and Sebalina (1966).

Russian genecology placed a different emphasis than any of the other schools on the importance of zonal and geographical variability. Typical is the work on populations of Onobrychis (Sinskaya 1958: 31-32). The Caucasian Onobrychis species, are, according to Sinskaya, difficult to classify along traditional morphological lines. But it is possible to distinguish vertical belt-populations on the basis of physiological characteristics such as flowering-times. Thus we get:

(1) The high mountain belt. Here plants are slow growing, early flowering, winter perennials;

(2) The middle-mountain belt. These populations have taller stems than is the case for populations in the high mountain belt. Also, most of the plants do not flower in the first year, and flowering occurs later in the season;

(3) The sub-mountain belt. These populations are late-flowering spring perennials;

(4) The adjacent steppe belt. Here all plants flower in the first year and are drought resistant, spring perennials.

The second novel element in the genecological writings of Sinskaya is the stress on biotic factors and their influence in the development of plant races. Thus, for example, in their study of the flaxweed (Camelina sativa), Sinskaya and Beztuzheva (1931) were able to show that flaxweed imitates the races of flax on which it grows and that intraspecific variations in the group are dependent upon adaptations both to climate and biotic influences.¹⁸ Genecologists in Scandinavia, America and Britain had paid little attention to the role of biotic factors in adaptation and it was this aspect of Russian genecology to which Gregor paid most attention in his 1944 review of the ecotype concept (Gregor 1944: 25-26).

It is interesting to speculate on why these distinctive features developed in Russian genecology. It seems possible that one reason for the neglect given to biotic factors and their influence on adaptation within the species by Western genecologists was due to the influence of synecological writings in their research.

18. For a brief English account of this research see Clausen, Keck and Hiesey (1948: 121).

Synecologists in America and Britain were strongly influenced by Clements' work on climatic climaxes and his stress on the importance of climate in explaining vegetation distribution and cover. British and American genecologists appear to have accepted this aspect of Clements' work, even where they rejected his neo-Lamarckian views on speciation. Indeed, the whole question of the relations between synecology and genecology is one which has been neglected by historians of ecology and which requires more analysis. However, this is not a theme which can be developed further within the context of the present study.

Alternatives to the Genecological Hierarchy in Biosystematics

The ecotype system and derivatives from it (e.g. the cline and deme terminologies) has been the most important of the classification hierarchies used by experimental taxonomists. However, the period after 1930 saw several fresh attempts to construct a system of classification for experimental taxonomy. The starting point of most of these efforts has consisted of an attempt to redefine the species-concept in a more "objective" manner, by recognising that a variety of different kinds of species exist which are definable by cytological and genetical criteria. We shall consider three examples of such classification systems - the comparium - convivia terminology of B.H. Danser, the genetic species of the British plant geneticist Cyril Darlington, and the biosystematic, population categories of W.H. Camp and G.L. Gilly.

(1) The Comparium, Commiscuum and Convivia

The Dutch taxonomist and geneticist B.H. Danser (1929: 339) introduced these terms to provide a set of experimental categories which could be defined on a non-morphological basis. Capacity for gene-exchange is the major criterion used to define these units. Thus we get:

The Comparium: all individuals which can hybridize regardless of the fertility or sterility of the product of the cross;

The Commiscuum: all individuals within a comparium which can freely exchange genes;

The Convivia: those groups of individuals within the commiscuum which can freely exchange genes but which are isolated by geographical barriers.

In practice this system has been rarely used. The commiscuum is practically synonymous with the term "ecospecies" as it was later defined by Turesson. The comparium was used by Clausen as a unit above that of the coenospecies (see Clausen, Keck and Hiesey 1945: 63-64).

(2) Darlington's genetic species

Darlington (1933: 813-814) distinguished six different kinds of species according to their cytology and genetic-reproductive mechanism. Thus, we get:

- (a) The habitually self-fertilized diploid;
- (b) The habitually cross-fertilized diploid;
- (c) The sexually reproducing fertile polyploid;
- (d) The mixed species containing both diploid and polyploid forms;
- (e) The complex-heterozygote species (balanced lethal type), as in Oenothera;
- (f) The clonal species which does not reproduce sexually at all.

Darlington introduced this division of the species in terms of the genetics of the breeding system because, he argued, different patterns of variation could be expected in each of these groups. It was the purpose of the taxonomist and cyto-taxonomist to elucidate what these different patterns of variation might be (Darlington 1933: 814).

3. The Biosystematic terminology of Camp and Gilly

In the same paper as that in which they introduced the term "biosystematy", Camp and Gilly (1943) also put forward a complex set of terms designed to remove the subjective term "species" altogether and replace it with categories based upon genetics, cytology and evolutionary data. Thus, Camp and Gilly maintained that the species of classical taxonomy could be divided as belonging to one of twelve new categories defined as follows:

- (a) homogeon: a species which is genetically and morphologically homogenous, all members being fertile;
- (b) phenon: a species which is phenotypically homogenous and whose individuals are sexually reproductive, but which is composed of intersterile fragments;

(c) paragenon: a species with relatively little morphological or genetical variation throughout its range, but which contains some aberrant genotypes. All its individuals are interfertile.

(d) dysploidion: a species composed of morphologically similar members of a dysploidon series, the individuals of which are sexually reproductive.¹⁹

(e) euploidion: a species whose individuals are sexually reproductive and which is composed of segments with a common origin arranged in a euploid series; the segments are morphologically separable although similar in appearance, but, because of different responses in various environments, appear to intergrade.²⁰

(f) alloploidion: a species derived by allopolyploidy, its individuals, although highly variable, are interfertile.

(g) micton: a species, often of wide distribution, the result of hybridization between individuals of two or more species; all individuals are interfertile with themselves and with the ancestral genotypes.

(h) rheogameon: a species composed of segments of reasonably marked morphological divergence whose distributions are such that gene interchange may take place in sequence between them; individuals of contiguous segments are interfertile.

(i) cleistogameon: a species which, in part, reproduces by means of cleistogamy.²¹

(j) heterogameon: a species made up of races, which, if self-fertilized, produce morphologically stable populations but when crossed may produce several types of variable and fertile offspring.

(k) apogameon: a species containing both apomictic and non-apomictic individuals.

19. "Dyploid series" refers to groups wherein there exists a series of chromosome numbers either greater or less than the expected number.

20. In a euploid series the plant populations have each of the different chromosomes of the set present in the same number and, therefore, possess an exact multiple of the haploid chromosome number.

21. Cleistogamy is the process whereby flowers may sometimes set seed without the flower opening or pollination taking place.

- (1) agemon: a species containing only apomictic individuals.

Camp and Gilly's proposals represent the most ambitious effort yet devised to divide the species into its component genetic and evolutionary types. Similar, but more recent, attempts to formulate classifications of an analogous kind are found in the work of Lamprecht (1959) and Alvarez-Lopez (1957).²²

In general these attempts to distinguish kinds of species according to genetical and evolutionary criteria have won little popularity, either in experimental or in orthodox taxonomy. It would appear that the different kinds of genetic and evolutionary situations that they were designed to represent are too manifold and complex to be accommodated within any single taxonomic framework. However, the persistence of such attempts shows that the trend away from the activity of classifying which is discernible in genecology after 1935 was by no means a universal one amongst experimentalists.

Genecology and Biosystematics since 1950

It is not intended here to deal in any depth with changes in genecology and biosystematics in the period since 1950. However, in order to relate the historical material of the last three chapters with the account of modern research in taxonomy represented in chapter one, a brief survey of some of the major developments in post-1950 biosystematics and genecology is in order. This account is not intended to be a definitive or exhaustive account of these developments.²³

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22. Lamprecht's paper is a far reaching attempt to recognise different kinds of species formally by making appropriate additions to the normal binomial nomenclature. Alvarez-Lopez argues that species are of three kinds: euspecies, which are groups with marked morphological and genetical differences; genospecies, in which genetic differentiation has occurred but morphological markers are slight or absent; and morphospecies in which morphological differentiation is marked but is associated with weak or non-existent genetic barriers. For a discussion of both papers see Davis and Heywood (1963: 460-461).
23. The two best recent reviews of trends in biosystematics and genecology since 1945 are those of Raven (1974) and Heslop-Harrison (1964). Both accounts stress the way in which experimental studies of species since 1950 have had as their objective the study of evolution as a process rather than classification.

Experimental studies of evolutionary processes with taxonomic revision as a major or auxiliary objective have remained an important element in plant science. Further, America, Britain and Scandinavia have continued to be the most active centres of this research.²⁴ In Britain the work of J. Heslop-Harrison, V. Heywood, D.H. Valentine, and D.A. Wilkins have special importance in this field. In the United States detailed genecological investigations are being carried out on several plant genera including Gilia (V. Grant and his associates), Clarkia (H. Lewis) and Helianthus nuttallii (R. Long).²⁵ In Scandinavia work of particular interest is being undertaken by B. Lövkvist whose research has included a reinvestigation of some of Turesson's ecotypes with the inclusion of cytological studies of the populations (see Lövkvist 1962).

Most of the trends discernible in this research were present in the writings of experimental taxonomists prior to 1950. In particular, the debate which was initiated in the 1930's over the continuous or discontinuous nature of intraspecific ecological variation has remained a central problem throughout this period, sometimes engendering heated controversy (e.g. O. Langlet 1959, 1963; J.W. Wright and H.I. Baldwin 1957). The consensus of opinion in recent research is that both types of variation may occur, depending upon the underlying pattern of important ecological gradients. Where such gradients were very sharp, more or less discontinuous variation will be found; where they are continuous this will in turn be reflected in genotypical and phenotypical characteristics in the plant population. However, the relative importance of these two kinds of ecological variation is still a divisive issue.

Another trend in modern experimental taxonomy apparent in the earlier work, especially of Gregor and his associates, is seen in the continuing discussion of the role which taxonomic objectives should

24. The continued dominance of American and British botanists can be seen from an analysis of the citations in Heslop-Harrison's (1964) review. Of the 35 authors with two or more papers cited 12 are American, 18 British and 3 Scandinavian.

25. An account of the work of Grant and his associates is given in chapter 6. For the work on Clarkia and Helianthus see Lewis (1957) and Long (1966).

play in research on speciation and intraspecific variation. Here, as Raven (1974) correctly emphasises, there is a growing consensus that biosystematical data do not lead to an unequivocal definition of the taxonomic units in most cases and that they do not dictate taxonomic decisions. Heslop-Harrison, writing in 1953, described this trend:

Recently, there has been a tendency among more radically minded evolutionists to deplore the "taxonomic" attitude in their science - the attitude which seeks to detect and define and classify "types", be they "eco-", "topo-", "cyto-" or of other form, rather than to study processes. Looking past the conflict of categories which has proceeded in the field of experimental taxonomy, we may perhaps glimpse a future in which defining of categories has been abandoned altogether, and experimental study of natural variation proceeds without "typification".

(Heslop-Harrison 1953: 121)

According to Raven (1974: 178), in the 25 years since the publication of Heslop-Harrison's New Concepts in Flowering Plant Taxonomy, this view has become one held by the majority of biosystematics and genecologists. However, here again, opinion is still divided. The sensitivity of this issue is shown by the fact that when, in 1962, the announcement was made that the biosystematics committee of the International Association of Plant Taxonomists had recommended the setting up of a separate International Organization of Biosystematics, this prompted worried letters to Taxon that an artificial division was being created within plant systematics (see Tryon and Wallace 1962).

A third trend within genecology since 1950 has been the search for physiological variation which is of an adaptative and ecological kind. A particularly interesting example of this trend has been the work on lead tolerance in Festuca ovina which has been carried out in Wales by A.D. Bradshaw and D.A. Wilkins (Bradshaw 1952; Wilkins 1957, 1960a, 1960b). Lead is normally highly toxic to this species, yet lead-tolerant races are found on mine-soil tips. Using an assay method based on the growth of adventitious roots in vitro and under uniform conditions, Wilkins was able to show that three races of Festuca were present: intolerant, medium tolerant and highly tolerant. Genetically, the property of tolerance is dominant and may be controlled by a single locus. An interesting facet of these investigations was that no morphological features could be found which separated the populations; they are

physiological races within the species but lack any apparent morphological markers.

A fourth trend within genecology is also evidenced in Bradshaw's work on another grass species, Agrostis tenuis (Bradshaw 1959, 1960). This is the tendency towards studies of small-scale genecological differentiation. Bradshaw was able to show, using techniques of experimental cultivation in both standard and varied environments, small-scale differences in physiology and morphology between 33 populations of this grass growing in Wales. These variations were adaptive and could be correlated with environmental factors, although in Bradshaw's opinion they were of too minor a character to warrant taxonomic recognition, either as clines or as ecotypes. Very little work of this kind has been done, and it seems a likely area for future genecological research.

A sign of the increasing status of research in experimental taxonomy was the foundation, in 1962, of the International Organization of Biosystematics, whose first President was the Icelandic cyto-taxonomist Askeff Löve. A further sign of the increasing importance and stature of this type of research is the publication in recent years of several undergraduate textbooks dealing exclusively with the subject of biosystematics - most notably those by Heslop-Harrison (1953), Solbrig (1966, 1970) and Briggs and Walters (1969). In addition, it is now usual for even more orthodox textbooks on systematics to devote considerable space to biosystematics and genecology (e.g. Davis and Heywood 1963; Heywood 1967).

Turning from genecology and biosystematics to more general trends within taxonomy as a whole, it is now possible to see that the "new systematics" of the 1930's and 40's was only the first in a series of innovatory approaches to classification which have been a persistent feature of plant classificatory sciences during this century. More recent challenges to traditional taxonomy have come from chemotaxonomy and, most notably, from the numerical taxonomy of Sokal and Sneath (1963). A brief discussion of the latter approach to classification is given in Appendix A. Certainly, the controversy surrounding these new techniques has been just as great, and in many ways parallels, the controversies which developed around genecology and biosystematics in the 1920's, 30's and 40's.

Discussion: Combinational Strategies in Species Making

Much of the most highly credited work which has been done in taxonomy since the 1930's has involved a method for applying the term "species" which involves neither using a cluster of identifying descriptions (Description theory) or rigid application of a single criteria (essentialism). Rather, combinational strategies have been employed.

Clausen and Babcock represent two experimental taxonomists who employed a strategy of this kind. A combinational strategy works as follows. Firstly a morphological classification of the genus in question is made or, if a modern treatment of the group exists, accepted as provisionally correct. Then biosystematical data is accumulated on the group under study (which is usually a genus or section of a genus). It is at this stage that ecological transplants will be made, chromosomes counted, and populations crossed in experimental gardens to study fertility relationships. If the evolutionary and phylogenetic data accumulated agree with the groups classification in terms of purely morphological considerations then the original classification is left unaltered: indeed, it is vindicated. However, if the new data appears to be at variance with the classification made along traditional lines then a new morphological classification is attempted. The groups morphology is re-examined with an eye to finding correlations between the groups morphological characteristics and the newly acquired biosystematic evidence. If such correlations are discovered then a taxonomic revision of part or whole of the genus is undertaken. However, if morphological markers cannot be found then the old taxonomic treatment is left unaltered, as being the best available.

In philosophical terms combinational strategies are very "messy". The resulting classification is neither truly phenetic (i.e. based on overall resemblance) or phylogenetic. It is not truly phenetic because genetical and cytogenetical data are heavily weighted in such an approach. Moreover, the desirability of such weighting is an a priori commitment in taxonomy of this kind. However, the classification adopted does not accurately reflect cytological and genetical "essences" either. Indeed in cases where the identifying description (in terms of morphology) is at variance with chromosomal and genetical data, it is the former rather than

the latter which is ultimately given precedence.

Although combinational strategies have been largely ignored in philosophical accounts of classification, they represent the only way of incorporating evolutionary data into taxonomy in a manner which is acceptable to the aims of orthodox taxonomists. And it is notable that the best example of work of this kind, e.g. Clausen's researches on Potentilla and Babcock's on Crepis have been widely approved of by both orthodox and experimental taxonomists. At the present time combinational strategies look like becoming the most widely accepted way in which evolutionary data can be given recognition in scientific classifications of biological natural kinds. The question of why this approach is widely approved of in spite of its apparent ad hocness on theoretical grounds opens up the general question of how different strategies of classifications are justified and maintained. This is a topic which will be considered in chapter 6.

Summary and Discussion: The Species Concept from 1930 to 1950

As is clear from the preceding discussion genetical and cytological evidence became increasingly important in theoretical discussions about species after 1930. Many experimentalists held, and still do hold, that genetical criteria (i.e. tests of fertility and sterility) are the only objective basis by which real (biological) species can be delimited. However, many taxonomists have continued to challenge this interpretation. The latter position is well summarised by Heywood in his textbook Plant Taxonomy.

Although isolating mechanisms are of great evolutionary importance since they allow populations to build up differences and evolve as independent units, the groups of plants which we recognise as species are in practice defined largely by morphological criteria. In very many cases there is a high degree of correspondence between morphological differentiation and inability to interbreed, but the two are not necessarily correlated ... (V)arious degrees of fertility may exist between members of different populations of the same species.

(Heywood 1967: 56)

So there is at present no universal consensus that genetical data provides an unambiguous criteria for defining what is meant by the

term "species". What about cytological evidence - does this provide a criterion for distinguishing species?

In fact, whether or not cytological evidence should be used in this way has been a source of contention in the recent literature on cyto-taxonomy. The form these arguments have taken is best illustrated by an example. Thus, we may consider the recent controversy between the English cyto-taxonomist I. Manton and the Icelandic cyto-taxonomist A. Löve.

The usual treatment of the discovery of chromosome races within the Linnaean species (i.e. the discovery that individuals which were previously regarded as members of the same taxonomic species have different chromosome numbers) has been to keep the members within the same species, unless good morphological markers can be found to correlate with the observed difference in chromosome number. This was the position which Clausen adopted in his work on polyploids and the same position was taken by Manton (1934) in her treatment of chromosome races within the Linnaean species Biscutella laevigata L. There were at least three chromosome races in this species - one hexaploid, one tetraploid and one diploid. However, Manton was unable to find any morphological differences between these populations and concluded that no taxonomic revision was possible in the group.

It was this last claim that was challenged by Löve (1951). According to Löve different chromosome "races" within the species always can be separated on morphological grounds, even if the morphological differences are only slight. And he argued that such forms should always be given taxonomic recognition as separate species:

Cytologists observing differences in chromosome numbers within some collective species are rendering little service to scientific taxonomy by reporting them only as new cases of "intraspecific polyploidy" and examples of lack of morphological characters of taxonomical value for separating the biologically isolated groups. Before publication they should always send good herbarium sheets to an able taxonomist ... In most if not all cases he will be able to tell the cytologist that his "intraspecific" types have previously been separated as species, or ought to be classified as such based on some major or minor morphological differences, perhaps not observable at first glance to the untrained eye.

(Löve 1951: 283)

However, this recommendation was challenged by Böcher who, like Manton, had worked on groups where morphological markers were very hard to correlate with chromosome number. In a summary of their research on one of these groups Böcher and his associates concluded that "we cannot accept the view of Löve that all types differing in the number of chromosomes should be classified as distinct species" (Böcher, Larsen and Rahn 1953: 301). More generally, Davis and Heywood have argued that cytological data should, for taxonomic purposes, be given the same weighting as data from any other source:

A special role is claimed for cytological data in taxonomy since the chromosomes are the seat of the hereditary material. From an interpretative viewpoint this claim is justified, but chromosome number and morphology as comparative data have to be considered on a par with other kinds of taxonomic evidence.

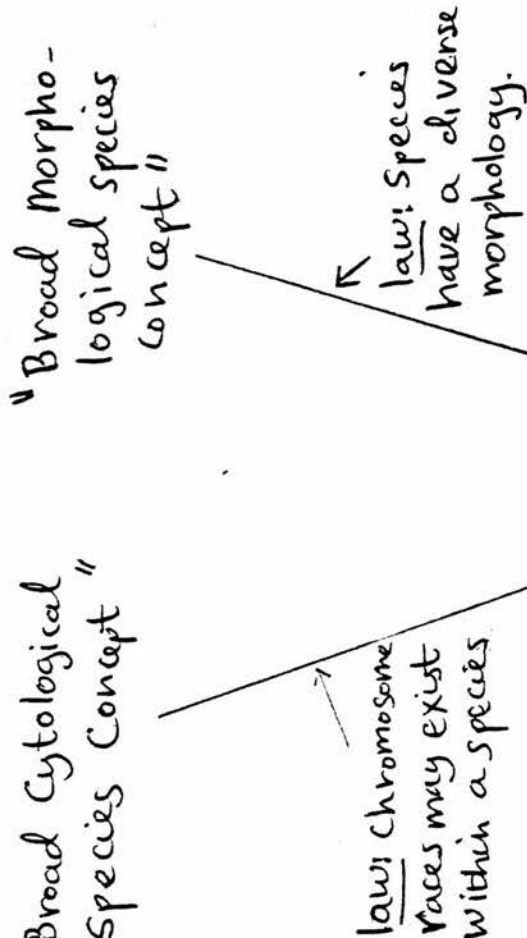
(Davis and Heywood 1963: 193)

And Turrill (1958) advanced a similar argument at a symposium on cyto-taxonomy held by the Linnaean Society of London.

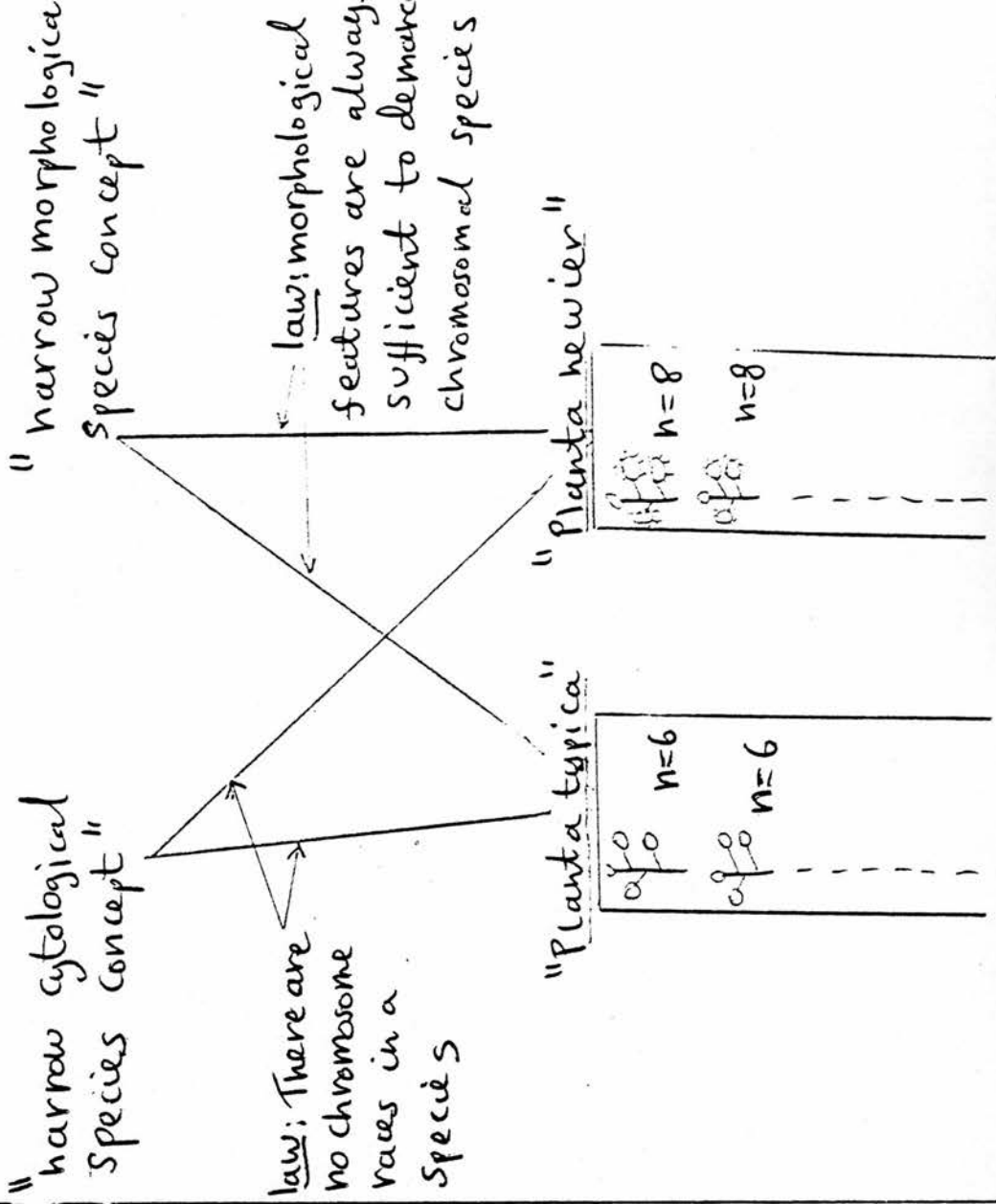
The question of whether chromosome populations should be treated as separate species has a direct bearing on the philosophical models of classification outlined in chapter 2. In terms of the network model of classification the positions taken by the two sides can be illustrated as in figure 5.7. For the sake of illustration an imaginary case is presented here involving a Linnaean species ("Planta typica L.") previously thought to have a chromosome number $n = 6$. A "race" of P. typica is discovered with a chromosome number $n = 8$ and with minor morphological differences as well (slightly hairy leaves). However, it is to be imagined that this morphological marker is not a "good" one in the taxonomic sense, e.g. suppose the "hairs" are so small that they are only visible with an electron microscope or that a few cases are found where "hairy" plants have a chromosome number of $n = 6$ and vice versa. Should the "P. newiensis" population be considered as a part of "P. typica" or not. Presumably for Putnam "P. typica" and "P. newiensis" are two different natural kinds (on all possible worlds!). However, for a description theorist, and especially one of the Searlian kind, a single difference such as chromosome number should not be used to separate the two types if they bear all or most of their other properties in common. From the network theorist's point of view either

Figure 5.7. Two Strategies for Dealing with the Problem of Chromosome Races within the Linnaean Species

A. Solution Proposed by Manton (1934)



B. Solution Proposed by Löve (1951)



treatment is possible. It so happens that the majority of botanists would probably agree with the "Mantonian" treatment of this case rather than the "Löbian" one. However, there is nothing in the nature of the "facts" or in the "logic" of the arguments used which forces adoption of either view.

To summarise: genetical and cytological data have become increasingly important in modern experimental research on classification. A number of attempts have been made to use genetical data (sterility and fertility) and cytological data (chromosome number) as rigid designators of the natural kind term "species". However, a great many taxonomists, both of the herbarium school (e.g. Davis and Heywood) and of the experimental school (e.g. Clausen, Turrill, Manton, Böcher) have denied the possibility of using genetical and cytological evidence in this fashion. In Putnam's terms scientists in this latter camp are presumably acting irrationally or illogically, because genetical and cytological evidence is the nearest we have to hidden essences in plant and animal natural kinds. However, from the point of view of the network model of classification, neither group is acting in a manner which is "illogical" or "irrational". Whether scientists wish to use genetical or cytological data to rigidly designate natural kinds is a point which they themselves must decide. There is nothing in the "logic" or semantics of a historical natural kind terms usage which gives one position precedence over its rival. Essentialism is a strategy of concept application. Whether, in any one instance, it is a good strategy is not a matter which can be given over to a priori considerations. These are problems which the scientist himself must decide.

A second interesting facet of recent discussions concerning classification at the species level has been the various attempts to restrict the term "species" to one or other of its "biological" or "morphological" senses. Two of these attempts have been dealt with already and so need only be briefly reviewed here. Thus Camp (1951) recommended that morphological species should be termed "binoms" and that the term "species", if used at all, should be only employed in its biological sense. Similarly, but in the opposite direction, Gregor and Gilmour introduced the "deme" terminology partly in order to remove the term "species" from the units of experimental

taxonomy and restrict its usage to herbarium taxonomy. A notable feature of these attempts to restrict the meaning of the term species is that none of them have enjoyed widespread popularity or currency amongst either experimental or orthodox taxonomists. The deme terminology has been little used by genecologists and, similarly, Camp's term "binom" has not replaced the term "species" in the floras and manuals of the herbaria. As Grant (1971: 31-36) has pointed out in a recent discussion of the literature pertaining to these efforts at nomenclatural reform, this failure has not been due to any fault in the logic of reasoning behind such prescriptions. In terms of clarity of exposition and "logical" use of language it would be an excellent idea to restrict the term species to either its morphological or biological sense. However, efforts to bring this situation about ignore the strong commitment which different research groups can have in using and deploying the same term. Language, like culture, is a resource and, like any resource, people are loath to throw it away or donate it as a gift to someone else. As Grant succinctly put it, attempts to restrict the term species "stand little chance of becoming adopted because, in each case they ignore long-standing historical claims on the term species by one or another large group of workers" (Grant 1971: 36).

Linked to these ongoing debates over the meaning of the term species there has also been, since 1935, a continuing failure amongst experimental taxonomists to agree on a common objective or goal for their discipline's development. Experimental taxonomy as conceived by Hall and Clements had a two-fold objective, namely, 1) to account for the processes whereby "natural" units arise in wild populations and 2) to classify these units on the basis of the information gained. Some later workers (e.g. Clausen, Camp and Gilly) kept to these two aims, but others (e.g. Gregor) have seen these two objectives as being, in some ways, incompatible.

The objectives of experimental taxonomists have affected the stance which they have taken towards traditional taxonomic practice. The early experimentalists were very critical of orthodox taxonomy; in the writings of later taxonomists the strategies adopted towards orthodox methods were more diverse. Some experimentalists (e.g. Grant and Camp) have remained highly critical of orthodox systematics;

others (e.g. Clausen and Gregor) adopted a more lenient approach. Two factors seem of special importance here. Firstly, some experimentalists came to the conclusion that mutual exchange of information between the two camps would be of benefit and this encouraged a rhetoric in which the traditional skills of the taxonomist were not devalued. This is especially evident in the writings of the Carnegie school where the team of workers included "alpha taxonomists". Secondly, the controversy within experimental taxonomy over the relative importance of continuous and discontinuous patterns of intraspecific ecological variation has also had a bearing upon this issue. Genecologists such as Gregor who emphasised the clinal nature of such variation saw in the desire for experimentalists to find classifiable units in nature an obstacle to progress. The natural result of such a view is to urge the separate development of the two disciplines of orthodox and experimental taxonomy and this is a position which is strongly advocated in Gregor's later research. For Gregor orthodox and experimental taxonomy were two related but separate concerns, each valid in its own sphere, but possessed of different aims and objectives. We have turned full circle from the early imperialistic claims of experimentalists dealt with in the previous chapter.

The methods of experimental taxonomy have also become increasingly diversified since 1930. Between 1920 and 1930 transplant studies had been the major method of experimental taxonomy. After 1930 these remained important, but newer techniques, such as breeding tests to establish fertility relations and cytological studies of the chromosome complement, also gained increasing currency. This diversity of technique was also reflected in the wider backgrounds of those entering the field after 1930. In the 1920's experimental taxonomists and genecologists had backgrounds in ecological botany or phytogeography. Experimentalists active after 1930 came from a number of background disciplines. Some, like Clausen, Böcher and Babcock were primarily cytogeneticists by training. Others (e.g. Turrill, Camp and Heslop-Harrison) had been trained in herbarium taxonomy and either learnt the laboratory skills associated with experimental taxonomy or worked in collaboration with experimental biologists (an example of the latter is Turrill's collaboration with the cytologist E.M. Marsden-Jones). Still others (e.g. Gregor and Sinskaya) had moved

into genecology from a background of research in applied aspects of plant breeding.

The increasing diversity of methods and aims in experimental taxonomy in turn also reflects the very wide diversity of approaches now manifest with plant taxonomy as a whole. The evaluation of such new approaches to classification as chemotaxonomy and numerical taxonomy is likely to occupy plant systematists for many more decades.

Chapter Six: The Role of Interests in the Development of Systems of Classification part one: the Role of Interests in Technical Prediction and Control.

In Chapter 2 some general models of classification were described which were taken from current philosophical debates about the nature of extension and reference. These models were treated as naturalistic i.e. as attempts to describe how scientific classifications have actually been formulated, modified and sustained. With the empirical material of Chapters three, four and five now presented it will be of value here to summarise the major findings which have resulted in treating philosophical theories of classification in this naturalistic way. In carrying out this task we shall focus mainly on classification of natural kinds at the species-level. Other levels of the taxonomic hierarchy could be used but it is on the question of the nature of species and how they should be delimited that controversies between different groups of systematists have been most acute.

The first point which emerges from the empirical material presented so far (and which will be further demonstrated by more material in this chapter) is that there is no agreed procedure for classifying species or even for defining what is meant by the term "species". In very broad terms, two main classes of species definition have been employed in botanical systematics: definitions using manifest properties of morphology (morphological species definitions) and definitions using reproductive criteria (biological species definitions). And it follows from this that the extension of any given species is not pre-determined in advance. Two plants may share most of their important morphological attributes in common but be members of different species in the biological sense. Conversely, two plants may be fully fertile but strikingly different in their morphology (indeed they may even on occasions be members of different genera).

Secondly, it will also now be clear that even working within one of these two main definitions of the species, options remain open. This is most obvious in the case of procedures for classifying species based on morphology, where species delimitation is notoriously subjective. Thus, morphological taxonomists themselves may employ broad or narrow morphological species concepts. They may be "lumpers" or "splitters".

However, the point is equally true of procedures for delimiting species along biological lines. All types of fertility relationships are formed in nature from complete fertility to complete sterility. Indeed it was to take account of this that led biosystematists to recognise different types of species in a genecological hierarchy (the coenospecies, the ecospecies etc.). But even within these units choices still remain. Consider the different uses of the term "ecotype" in genecology. Turesson used the term originally to cover ecological races within the Linnaean species which were local populations. The ecotypes of Clausen were studied in populations covering a much wider geographical area and delimited regional populations. And still others (e.g. Gregor) have maintained that ecological populations within the species grade continuously into one another in most cases. On this view the ecotype is a range on an ecocline and can only be more-or-less arbitrarily designated as a separate unit.

This then is the first major conclusion which follows if philosophical theories of classification are treated naturalistically: the extension (and hence the meaning) of natural kind terms is not pre-determined in advance. The second major finding is that description theories of meaning and essentialist theories describe strategies of classification procedure. This point has already been made for each of the major figures discussed in Chapters three, four and five. However, it is worth stressing again here because it opens the question of the criteria by which different strategies of classification are selected and developed.

It was argued in Chapter two that classifications are conventions and the network model of classification developed from the work of Mary Hesse was used to illustrate the possibilities of this approach. In this chapter it will be argued that a conventionalist account of classification is of value in understanding two key aspects of the historical material presented in the last three chapters:

1. As a framework for understanding the nature of the controversies which took place between orthodox and experimental taxonomists.
2. As a framework for understanding the controversies that developed within experimental taxonomy over the question of how new species evolve.

We shall now examine each of these topics in turn, showing also how the empirical material can be used to give further insight into the nature of the network model of classification itself.

As we have already seen, the response of herbarium taxonomists to the sometimes extremely critical attacks of experimentalists on their methods, procedures and results has been varied. However, a marked feature of this response has been that there has been no wholesale abandonment either of the Linnaean system of nomenclature or of the procedures by which plant species are described, catalogued and named. The categories of the Linnaean system (class, order, species etc.) have continued to find employment in monographs and floras; herbarium taxonomists have continued to insist that different species, to be so-called, must exhibit clear-cut morphological distinctions which allow their separation from related species.

It is a point of great interest that where orthodox taxonomists have had to justify their continued adherence to traditional methods of taxonomic practice they have usually done so in pragmatic and instrumentalist terms. For classification accurately to reflect the evolutionary or cytogenetic aspects of a plant's history is seen as laudable in its own right, but on practical grounds it is denied that this objective can or should always be acted upon:

Classification should not be inconsistent with what evolutionary evidence is known, although there may be instances where it may be more convenient and serve more purposes if it is.

(Davis and Heywood 1963: xviii)

And again:

If a general classification is going to be widely used, it needs to work. We must be able to place taxa in higher taxa so that we can find them again. This means that practical considerations, which mitigate against the 'objective' aspect of classification, are very important in systematics and necessitate that science shall come to terms with art if biological classification is to be of maximum use to science.

(Davis and Heywood 1963: 83)

As a rule orthodox taxonomists have not denied the value of experimental taxonomy for the production of "special purpose" classifications, but it is denied that such classifications should be seen as a replacement of the existing system. As the entomological

taxonomist T.D.A. Cockerell (1926: 588) put it in an early and generally enthusiastic review of Turesson's work:

(W)hile the ecotype system is highly illuminating, it should not take the place of definite names accompanied by precise descriptions and supported by the type specimens of the herbaria.

And they have pointed to the sheer practical difficulties which stand in the way of the widespread developments of experimental methods in taxonomy. The Norwegian phytogeographer Knut Faegri (1937b: 401), for example, says in another review of Turesson's work that:

The thorough taxonomic-genetical analysis of a genus, of its inner structure and relations to other genera ... is, if not always the work of a lifetime, at all events the work of many years' intense studies; in the case of trees perhaps the work of centuries. One can hardly expect taxonomists and phytogeographers to wait so long.

The fact that orthodox taxonomists usually legitimate their methods and classifications on pragmatic grounds has resulted in a tendency to see the units of experimental taxonomy as somehow more 'objective' or 'real' than those of orthodox taxonomy, and to perceive the classifications of orthodox taxonomy as having only a heuristic or instrumental value. Certainly there has been and continues to be a widespread tendency for experimental taxonomists to characterise the categories of orthodox taxonomy in this way (Hall and Clements 1923; Turesson 1930; Grant 1957; Dobzhansky 1958). As Dobzhansky puts it:

A systematic working with mammal or bird skins or with pinned insects or with dried plants in a herbarium has obviously no direct knowledge of whether the forms which he examines could or could not exchange genes. It would be preposterous to expect him to acquire such information before he classifies his specimens. Making a classification cannot be postponed; it is needed now as an aid to all other biological studies... The species of the systematist are inferences concerning the biological species which are the reality of nature.

(Dobzhansky 1958: 39; emphasis added)

However, it is worth noting that there is no necessity to regard the units of orthodox taxonomy in this fashion. As Davis and Heywood (1963: 94-95) point out in an interesting development of an argument first put forward by Valentine and Löve (1958), the units of orthodox taxonomy can be seen as just as 'real' as those of biosystematics.

The taxonomic species is often criticised by biosystematists on the grounds that it is less important biologically than species defined in terms of gene pools and sterility barriers. But ... this objection can be taken too far, since it would be absurd to underestimate the biological significance of the morphological (and physiological) differences between populations ... The form of a plant represents its response to its environment; it has come, in the course of evolution, to have leaves of just such a shape and flowers of just such a colour and to occupy a habitat in which the soil is of a certain texture and acidity. If another plant has leaves, flowers and habitat preferences which are all different, it is arguable that these differences are of at least as great biological significance as the ability of plants to exchange genes freely.

(Davis and Heywood 1963: 94-95).

The continued use of Linnaean taxonomy by orthodox systematists has meant that, for some groups at least, alternative or "competing" orthodox and experimental classifications now exist side-by-side. It is where competing taxonomies occur that controversy between orthodox and experimental taxonomists have often been most acute. This is especially the case at the level of the species where, as we have seen, the conflicting accounts employ different species criteria. For orthodox taxonomists, species are populations of morphologically similar individuals separated by visible morphological gaps from related species. For the biosystematist, species are normally defined as interbreeding populations of individuals, linked by a capacity for gene-exchange. In practice, especially in sexually breeding groups, these two conceptions of the species do not produce conflicting classifications (e.g. all human races are both capable of breeding with each other and morphologically distinguishable from related living primate species). However, frequently, and especially in plants with asexual or partly asexual breeding cycles, this is not the case. It is in these groups that competing taxonomies may be found. The nature of these competing taxonomies can best be illustrated by giving detailed consideration to some examples drawn from the historical literature.

Controversies in Classification in Plant Species Example 1
Spiraea ulmaria (ROSACEAE)

For details see Turesson (1925: 162-168). Turesson demonstrated by means of transplant studies that there were three ecotypes of this species

in Sweden: a coastal type with curved leaves, an inland type with straight leaves and long internodes between the leaflets, and an upland type from Central Sweden with shorter internodes. Systematists working on this material had previously recognised varieties on the basis of leaf shape and pubescence (i.e. presence and amount of hairs on the leaf). Both of these characters are well preserved and easily recognised in herbarium specimens. However, Turesson found that these characters were of little value in determining the ecotypes of ulmaria:

The treatment of spiraea ulmaria by systematists has resulted in a large number of forms and varieties generally based upon characters pertaining to the differences in leaf-shape and hairiness. The great majority of these systematic forms, however, are of no value for the grouping of ulmaria - populations of ecotypes ... Extensive cultures of material from widely different regions is needed before any understanding of the ecology of this species, as well as other species can be obtained.

(Turesson 1925: 168)

Thus, for example, the variety S. ulmaria var. denudata of the systematic handbooks, Turesson found to be present in all three ecotypes. Similar cases could be cited from many of the other genera on which Turesson worked.

Example 2 Madia citri-gracilis and its allies, Madia subsection eumadia (COMPOSITAE). For details see Clausen, Keck and Hiesey (1945: 22-45). Clausen and his co-workers first became interested in this group when they discovered a new species, Madia citri-gracilis growing at high elevations in California. The populations of this plant were found to have 24 pairs of chromosomes ($6x = 48$). This is an unusual number for this section of the Madia where all previous records indicated populations which were either diploid ($2x = 16$) or tetraploid ($4x = 32$). The likeliest origin for a population with 48 chromosomes was from a cross between a diploid and a tetraploid with subsequent doubling of the number of chromosomes (allotetraploidy). On morphological evidence the likeliest diploid ancestor for M. citri-gracilis was Madia citriodora, a species not previously treated taxonomically as within this subsection of the genus. The likeliest tetraploid was Madia gracilis. By means of artificial crossing between these two probable parental species, Clausen et al. were able to

synthesise M. citrigracilis artificially, providing strong circumstantial evidence in support of this hypothesis.

However, further research indicated that relations within this complex were even more complicated than this. Thus, further cytological study showed that M. gracilis was itself composed of two chromosome races. One of these, found at low elevations, had a chromosome number of $4x = 32$. The second population, which grew at high elevations, was hexaploid ($6x = 48$). Also, indirect evidence supported the conclusion that this hexaploid gracilis was itself derived by allotetraploidy from the tetraploid race of gracilis ($4x = 32$) and another diploid Madia - M. subspicata. Finally, hybridization experiments revealed that the two hexaploid populations (i.e. M. citrigracilis and hexaploid gracilis) could exchange genes. This rather complicated set of relationships is shown diagrammatically in figure 6.1.

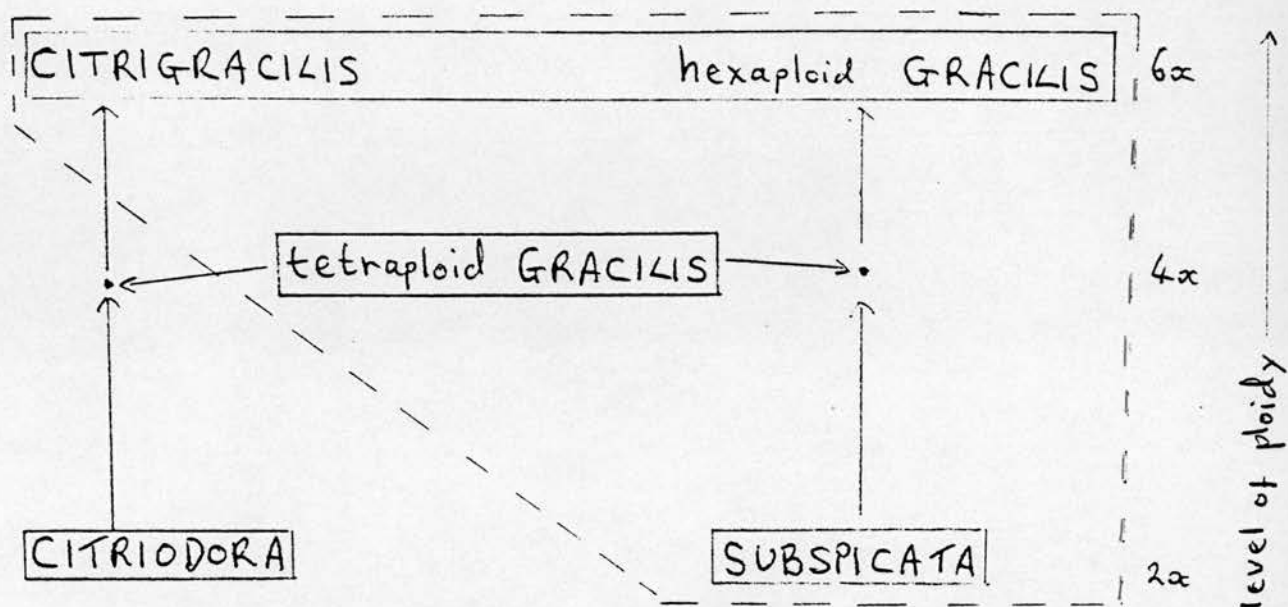
This example illustrates particularly well how species definitions, whether evolutionary, biological or morphological, can lead to different results when applied in critical cases. From the perspective of the phylogenetic or evolutionary viewpoint the complex can be split into 5 units, all of equal importance (Clausen, Keck and Hiesey 1945: 43). From a genetical viewpoint the two diploids and the tetraploid are distinct, but the two hexaploids, since they can cross and produce fertile offspring are one unit. From the morphological viewpoint only citriodora is very clearly set off from the rest, and Clausen, Keck and Hiesey found the two races of gracilis to be completely indistinguishable morphologically. These two populations could only be distinguished by chromosome counting.

In their actual treatment of the group Clausen, Keck and Hiesey (1945: 43-44) take none of these positions. Rather, taxonomic names are given to all populations within the complex except the two races of gracilis, which for practical reasons, are considered to be of one species.

Example 3 Phleum pratense and Phleum alpinum (GRAMINAE)

For details see Gregor (1931) and Gregor and Sansome (1930). These two grasses, recognised as separate species by Linnaeus, had long been known to be closely related and had sometimes been lumped together as a single species. However, Gregor and his associates, using genetical

Figure 6.1. The *Madia citrigracilis* complex (adapted from Clausen Keck and Hiesey 1945:43)



- - - - boundaries of morphological relationship
 ————— boundaries of gene-exchange
 —————> ancestral relationship of allopolyploidy

Table 6.1. Gregor's treatment of Phleum
(from Gregor 1931:212)

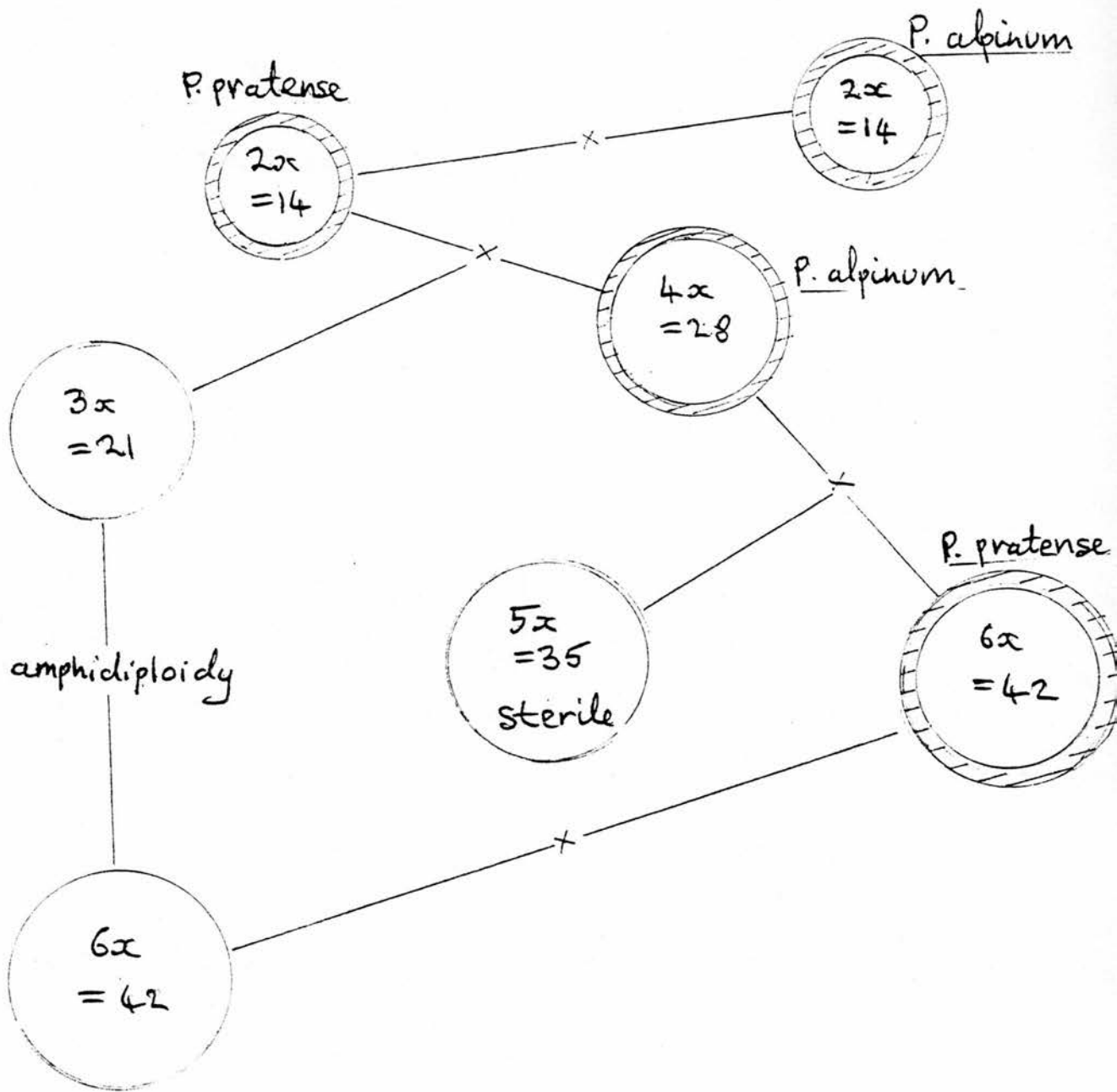
Coenospecies	<i>P. pratense-alpinum</i>
Ecospecies	<i>P. pratense</i> diploidium <i>P. pratense</i> hexaploidium <i>P. alpinum</i> diploidium <i>P. alpinum</i> tetraploidium
Ecotypes	<i>P. pratense</i> 2n prostratum " decumbens " ascendens " erectum 6n decumbens " ascendens " erectum

and cytological techniques, were able to show a pattern of complexity which had not hitherto been suspected on the basis of morphological studies. Thus Phleum pratense was shown to consist of two cytologically distinct races, one diploid in its chromosome number ($2x = 14$) and one hexaploid ($6x = 42$). Similarly, Phleum alpinum could be diploid ($2x = 14$) or tetraploid ($4x = 28$). By crossing diploid P. pratense with tetraploid P. alpinum, Gregor and Sansome were able to produce a synthetic hexaploid which was fertile with naturally occurring populations of hexaploid P. pratense. This led Gregor and Sansome (1930; 385) to the conclusion that the naturally occurring hexaploid race of P. pratense had probably arisen in an analogous way. In addition, transplant studies on Phleum pratense showed that there were at least 7 ecotypes and others were suspected to be present in the material of P. alpinum as well. The relationship between pratense and alpinum is shown in figure 6.2.

In his taxonomic treatment of the group Gregor (1931: 211-213) suggested that the two chromosome races of Phleum pratense, hitherto unrecognised by taxonomists, should be given specific, or at least subspecific, status. However, in his own classification of the group he used not the units of orthodox taxonomy, but the genecological system of Turesson (see table 6.1). On this view the whole complex represents a single coenospecies ('Phleum pratense-alpinum') with 4 ecospecies and at least 7 ecotypes.

This classification of the group elicited a sharp attack from A.J. Wilmott, a herbarium taxonomist working in the botany department of the British Museum at South Kensington in London. In his paper Wilmott (1932a: 49-50) attacked Gregor on the grounds that Phleum pratense and alpinum are separate morphological entities and that they should not, therefore, be united as a single "coenospecies". However, the wider implication of the paper is that, if progress is to be made in taxonomy, it will require not only that taxonomists become competent in genetics and cytology but also that geneticists must be competent taxonomists. Gregor's work on Phleum is cited as an example where this is not the case. Wilmott argues that taxonomists should take account of genetical criteria in deciding what counts as a species, but he denies such data any special significance:

Figure 6.2. Genetical and Cytological Relationships between *Phleum alpinum* and *P. pratense* (adapted from Gregor 1931: 209)



Key



Population found in nature



Population found in laboratory



hybrid cross attempted

The author (i.e. Gregor) forgets that apart from morphological characters there would be no genetics, for the geneticist is only formulating theoretical explanations of an observed morphological succession. The author needs to think in terms of the realities behind words. The Scottish Universities generally supply a philosophic basis, which seems to be lacking in this paper. After reading it P. alpinum remains an entity morphologically, distributionally and historically distinct from P. pratense.

(Wilmott 1932a: 49)

In his reply Gregor (1932) accused Wilmott of arguing that taxonomists should take account of information obtained from genetics and cytology, but of ignoring such data when, as in the case of Phleum, it suggested a treatment at variance with his pre-conceived opinions on the groups' taxonomic status. Gregor also pointed out that treating the group as a single species was in agreement with the conclusions of some previous taxonomists. Wilmott replied (1932b) that the taxonomist must be prepared to use genetical and cytological data when necessary, but that they should not be forced to employ it in the manner in which geneticists and cytologists wanted such data used. The controversy might well have continued, but A.B. Rendle, the keeper of the botany department at South Kensington and the editor of the Journal of Botany in which the interchanges appeared, stepped in and refused to publish any further correspondence on the issue.²

Example 4 Gilia inconspicua (POLEMONIACEAE). For details see V. Grant (1957, 1971: 31-33) and A. Day (1965). The plant genus Gilia is a group whose biosystematics and genetics have been the subject of a great deal of work in recent decades by Grant and his co-workers in California. We shall examine taxonomic problems in two "species" or "species-complexes" within the Gilia genus, these being Gilia inconspicua and G. tenuiflora.

As Day has demonstrated, the Gilia inconspicua complex consists of not less than five inter-related 'sibling' or 'biological' species. Three of these species are diploid with respect to their chromosome

2. Gregor sent Turesson offprints of Wilmott's article in the Journal of Botany and suggested that Turesson should write a letter criticising the paper for Nature. However, no publication of this type ever appeared. (Gregor M.S., letter to Göte Turesson, 6.4.1932), this correspondence is part of the Turesson archives at Lund University.

number, the remaining two are tetraploid. Analysis of the chromosome complement of each group showed that one of the tetraploids had been derived, by hybridization and doubling of the chromosome number, from two of the diploids (G. minor (2x) + G. clokeyi (2x) = G. transmontana (4x)). The other tetraploid is derived also in part from G. minor and in part from a third diploid G. aliquanta (G. minor (2x) + G. aliquanta (2x) = G. malior (4x)). Artificial hybridization shows that the five groups, although fertile in themselves, are highly intersterile in all combinations, so that biologically they are 'good' species. However, external phenotypic differences, while present, are not such as to allow identification in every instance. The tetraploid G. transmontana bridges the morphological gap between its two diploid ancestors so that clear-cut morphological differences do not occur. Similarly, G. malior intergrades morphologically into its two diploid ancestors. Also, since the G. minor genome is common to both tetraploids, these also cannot always be separated from each other on purely morphological grounds. In practice it is only with the aid of a microscopic examination of the chromosomes that we can distinguish any one of these "species" from another. Morphologically they form a single group. This situation is illustrated diagrammatically in figure 6.3.

Example 5 The Gilia tenuiflora-latiflora complex For details see Grant (1957). This group consists of at least 4 different "elements" which are quite distinct morphologically but also capable of gene-exchange. Apparently, at some time in the past, primary speciation began in this group but was interrupted by subsequent hybridization. The situation is illustrated in figure 6.4.

The taxonomic problems here are in many ways a mirror-image of the Gilia inconspicua case mentioned above. In this instance the rather striking morphological gaps between the constituents of the group would mean that the orthodox taxonomist would probably wish to retain them as distinct species despite the evidence of gene-exchange. Alternatively, for the strict adherent of a biological species concept, one is dealing here with only a single species. Grant's (1957) discussion of the group recommends that the Linnaean term species ought to be abandoned altogether in this particular instance. Instead he uses the term 'syngameon' to describe the whole complex and he refers to the individual elements

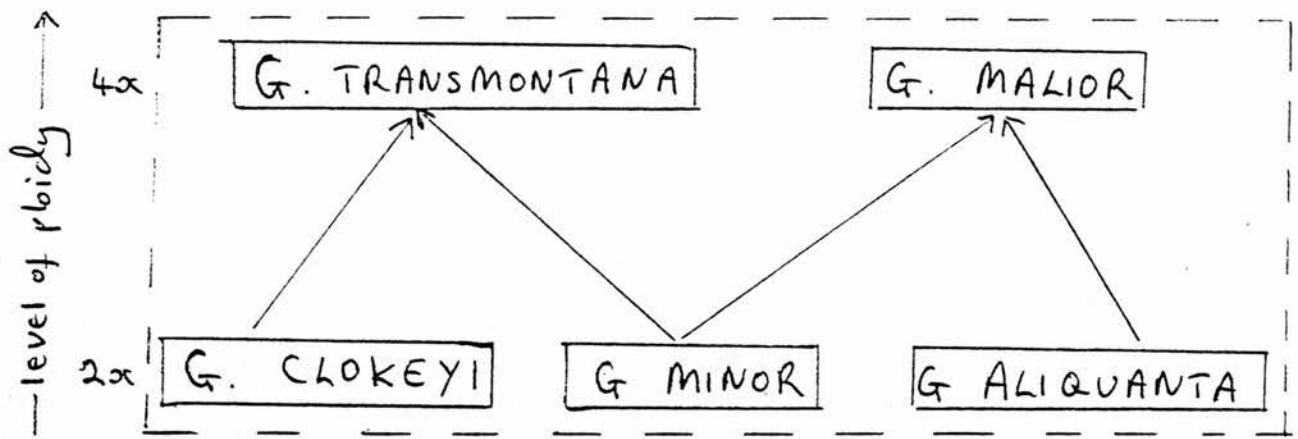


Figure 6.3. The *Gilia-inconspicua* complex

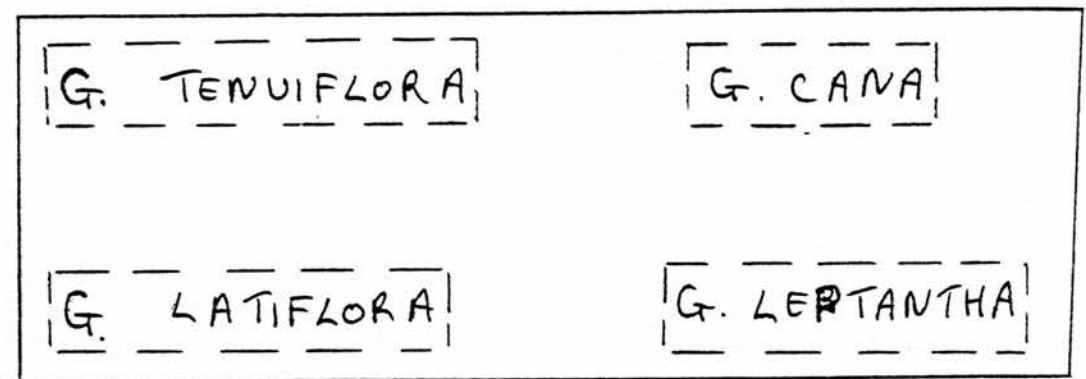


Figure 6.4 The *Gilia tenuiflora-latiflora* complex

Key to figs 6.3 and 6.4

- — — — boundaries of morphological relationship.
- boundaries of gene-exchange.
- ancestral relationship of allopolyploidy.

within it as 'semispecies'. For the formal taxonomist this does not, of course, present a viable solution and such an account would be at odds with the rules laid down in the International Code of Botanical Nomenclature; for according to that code, all individual plants belong to a species.

Problems like the ones in Gilia taxonomy outlined above illustrate again the issues which separate orthodox and experimental taxonomy. For the herbarium taxonomist species are units of morphological discontinuity. Practical concerns of identification necessitate that this shall be the case. The general point has been put by Davis and Heywood (1963: 461)

... if we are going to continue to employ the formal taxonomic hierarchy ..., the less we attempt to redefine its categories in evolutionary and genetic terms the better. To do so is to enter such a quaking bog of conflicting aims and interests that practical classification would be paralyzed.

And in their flora of the Pacific North-west C.L. Hitchcock, A. Cronquist and M. Ownberg (1959: 109) make the same point in a specific reference to Gilia and the work of Grant:

In such complexes ploidy level has little direct taxonomic significance and a proper taxonomic treatment must continue to be found largely on classical morphologic-geographic methods.

For the experimentalist operating with a species concept based upon capacity for gene-exchange such concerns are not sufficient to prevent splitting, say, a group like Gilia inconspicua into its component biological species. As Grant (1957: 57) rather scathingly comments:

The naming of sibling species as a result of biosystematic studies has provoked a certain discontent among many herbarium curators and floristic taxonomists. The biosystematist does indeed have a responsibility to determine and annotate as many large herbarium collections as is feasible. He also has a responsibility to science not to suppress those findings merely in order to facilitate the task of herbarium filing.

Nor should it be imagined that examples like the ones given above are exceptional occurrence and hence of little importance to most systematists. The modern period of biosystematic investigations (i.e. since 1950) has revealed ever increasing numbers of such problem

groups. Grant (1957: 53) argues that such taxa are the rule rather than the exception in higher plant taxonomy.

Discussion: Classification as Invention and the Role of Interests in Technical Prediction and Control

The material presented above is of general significance because it lends support to the view that classification is a process of invention rather than discovery, that our classifications of the natural world are 'made' rather than 'found'. If this is the case, then in an important, indeed fundamental, sense, classifications of the natural world have the status of conventions and are thus sustained and modified in response to changing patterns of social contingencies.

The further merit of these examples is that they lend support to this view in a context which in the past has been thought particularly supportive of the alternative view, viz. that there is a unique pattern of classification isomorphous with the real structure of nature. In the realm of plant and animal classification certain modes of approach have appeared as particularly distinct and obvious, certain ways of drawing boundaries particularly fundamental.³ However, here, as elsewhere, the natural world is so complex and rich in information that particular ways of drawing boundaries always involve selection and processing of information. The particular methods of selection and processing adopted in any one instance are, therefore, conventional in character, dependent upon prior commitments to certain shared objectives and concerns. To show that our classifications of the natural world have the characteristics of invention is strongly to support the notion that all systems of classification have such a character. To show that systems of natural classification are designed to serve and maintain shared interests and objectives is to suggest that classification is never a passive and disinterested process of discovery unrelated to social objectives and concerns. Attempts to classify the world of natural kinds have the status of being a 'hard case' for any theory of

3. This latter point is well illustrated in some of the recent work in botanical anthropology. When primitive tribesmen classify plants using morphological criteria the result often agrees closely with the species lists of herbarium taxonomists working in the same geographical area (cf Raven, Berlin and Breedlove 1971).

classification as invention to overcome, for it is in classifications of this sort that the instrumental and contextual concerns involved in the construction of all systems of classification are least evident and hardest to locate.

How can we evaluate competing taxonomies like those found in Spiraea, Madia, Phleum and Gilia? Is it possible to make a direct appeal to nature in order to evaluate the best taxonomy. Evidently, no. In these cases both taxonomies are conventions designed to emphasise different aspects of the real world. Consider again Gilia inconspicua, morphologically we do indeed find only a single species; experimentally, evidence can be accumulated whereby five different species may be discerned. Both taxonomies are built upon perceptible, systematizable, stable distinctions between individual plants. In this sense the natural order sustains both taxonomies; neither can be said to be erroneous. Nature does not in itself allow such an evaluation to be made.

As a philosophical problem the argument between realism and conventionalism has endless ramifications and appears to be doomed to indefinite continuation.⁴ Nor can every component of realist accounts of classification be dismissed at the level of naturalistic description (Putnam's work illustrates this point). However, at this level, the present examples do concern classifications which in many important respects do have a conventional, instrumental character and they indicate how, in these respects, classifications generally might be expected to have such a character.

A remarkable feature of the controversy over experimental methods in taxonomy is that the conflict between the two groups of scientists involved has led to no emergent consensus; thus in this respect the

4. For a recent statement defending a conventionalist account of scientific knowledge see Douglas (1975: ix-xxi). For a defence of the realist view of science see Hesse (1974: 283-382). In the mainstream of philosophy arguments between realists and conventionalists have been especially evident in the disputes over realist and nominalist theories of universals. For a brief but lucid account of this controversy see Flew (1971: 442-461).

present example seems to be at odds with other accounts of conflict in the history of science (cf. Kuhn's (1970) account of conflict and crisis revolution in the physical sciences.) On the contrary, questions concerning the value of experimental methods in taxonomy have continued to be voiced for over half a century, and many of the central issues remain quite as controversial today as they were fifty years ago.

This has been the case because the alternative systems of classification of orthodox and experimental taxonomy are designed to portray different aspects of reality and to satisfy different demands for technical prediction and control.⁵ Linnaean taxonomy has continued to flourish into the present century because it continues to serve particular interests in prediction and control not readily replaced by an experimental approach. It makes possible what Heslop-Harrison (1953: 10) calls the "primary survey" of the plant kingdom. However, because the method failed to satisfy these biologists concerned with a more detailed analysis of the mechanisms of evolution and speciation, alternatives to the Linnaean approach have been, and are likely to continue to be, formulated. To the extent that nature is conceived of as corresponding to the systems of classification which result, groups of professional scientists have sustained conflicting accounts of what natural kinds exist.

It would seem then, that whatever their rhetoric of justification, scientists in fact evaluate classifications in instrumentalist terms. At this point, therefore, we need to examine more closely the notion of "interests in technical prediction and control". Two points deserve special emphasis. The first is that the idea of interests in prediction and control cannot be used as a criterion for demarcating science from non-science or even "good" science from "bad" science. Certainly, interests in prediction and control have been important in the development of western science. But, history also is typically produced in a manner which lays heavy emphasis on its value as an instrumental body of knowledge (see Barnes 1977: 14-15). Neither are interests in prediction and control of the environment an exclusive feature of Western knowledge-systems. A

5. The notion of "interests in technical prediction and control" stems initially from the work of Habermas but is used here in the sense discussed by Barnes (1977: 1-26).

very strong case can be made for seeing the "magical" cosmologies of primitive societies as being primarily concerned with instrumentalist objectives.⁶

The second important feature to observe about interests in technical prediction and control is that they are dependent upon the social practices in which any given system of classification is embedded. In a different context from the present one Barnes (1978: 12) made this point in the following manner:

What activities and judgemental decisions would be indicated by an interest in prediction and control? ... Perhaps a philosopher might talk in terms of the root mean square reliability of all the generalisations on the net being maximised, and maintained at a maximum as new information becomes available. But such a notion makes no sociological or anthropological sense, and even a philosopher would be hard put to it to translate it into any plan for rational activity. As we know, this sort of thing does not happen at all. Rather interest in prediction and control is socially structured and focussed; it is always a function of a particular social context; wherein it is centred upon particular generalizations, and the reliability and scope of particular methods and procedures.

Thus, orthodox and experimental taxonomists deploy different craft skills and competences learned in different social networks and communities. And this in turn affects the instrumental evaluations which they make concerning their work. There is no objective point at which a given methodology becomes too expensive or too time-consuming for the results obtained to be no longer worth the labour and effort required. Rather what constitutes such a "doompoint" is itself a variable linked to the social interests and goals of the community and supported by the social matrix.⁷ For Faegri experimental methods in

6. This point is made particularly well in J. Willer's (1971) comparison of the belief-systems of magic, religion and science.

7. The notion of "doompoint" is taken from the work of the anthropologist Mary Douglas (see Douglas 1970).

taxonomy were too time-consuming and expensive to ever become the basis for most taxonomy. At best they could be used to provide insight into the nature of a few plant genera susceptible to such an approach. For Turesson, in contrast, it was the purpose of taxonomists to produce those classifications which would best serve the needs of biology as a whole, regardless of the effort and money involved.

Clearly the instrumentalist justification of scientific beliefs, as with the legitimation of belief in general, is only understandable from a sociological approach which is symmetrical in its style of explanation and impartial with respect to the truth or falsity of legitimation claims. In the dispute between orthodox and experimental systematists consensus has yet to be achieved as to which side is "right" or "wrong" and this makes the necessity for a symmetrical approach obvious. If the early experimentalists had succeeded in their stated aim of replacing orthodox taxonomy with an experimental approach, it is highly probable that the value of such a symmetrical approach would have been harder to establish. When, in a scientific controversy, consensus is achieved, whether by genuine synthesis or by fiat, the symmetry of the preceding dispute is masked. Often the realisation of this symmetry can only be reached by the most painstaking historical research and by a methodological willingness not to allow current beliefs to be the criteria by which past belief is compared, evaluated and judged. A controversy like the one between orthodox and experimental taxonomy, which is at once both a historical and extant phenomena, provides a demonstration of the value and correctness of maintaining such an approach.

To summarise then, the present case demonstrates the plausibility that the alternative classifications of orthodox and experimental systematics are conventions, chosen according to different prior interests in prediction and control. It is also clear that these different interests and the different craft skills and practices with which they are associated, affected not only which of a given set of classifications was selected or utilised in any given instance, but that they played a vital role in the actual construction of the classification. In an important sense the classifications took the form that they did because of the interests and objectives of those who constructed the classifications. In many important ways classification is a process of invention rather than

discovery. The form these inventions take is in turn influenced by socially focussed interests and objectives. Also, these in turn can be directed and changed by wider concerns in other communities and disciplines. Using the example of experimental systematics in botanical classifications it has been possible to locate how some of these changing social interests and concerns have been developed and modified. It is a point of some importance that none of these interests have been in any way scientifically inappropriate or in some way 'beyond the bounds' of science. In the traditional idiom of the history of science, the controversy between orthodox and experimental taxonomists has been 'internal' to science. And yet, as has been shown, the controversy remains intelligible only if science is considered as a human activity and if reference to such factors as socialization, patterns of reward, objectives and interests is taken into account. These are sociological issues. To deploy sociological explanation is not necessarily to do 'external' history of science or to show the influence of 'external' factors on scientific growth. Even in a case like this, without 'external' socio-political factors being particularly evident, a sociological approach is essential to an understanding of the development and distribution of different classifications of the natural world.

The major claim made in Chapter two, that the classifications of natural kinds are developed in ways which are not laid down in advance, has now been vindicated. What of the theories about how those natural kinds originate? The network, it will be recalled, incorporates all the terms used in a culture both "theoretical" and "observational". In the remainder of this chapter we shall explore the possibilities of the network model as a perspective for understanding theoretical divisions within taxonomy over the question of how natural kinds arise.

A Conventionalist Interpretation of Theoretical Divisions within Experimental Taxonomy

We have seen that the network model outlined in Chapter two is of value in understanding the controversies which took place between experimental taxonomists and orthodox taxonomists. However, as was shown in the historical material discussed in Chapters 3-5, not all the arguments about experimental systematics were concerned with this issue. There were considerable controversies within experimental taxonomy as

to the origins and mechanisms of speciation. Three of the theories which were prevalent after 1900 were as follows:

1. That there existed a fixed number of basic underlying species, subsequent forms being derived from these by hybridization. This was the "hybridization theory" of Lotsy.

2. That new forms of "adaptants" arose by the direct action of the environment on the plant form (ecogenesis) and its subsequent fixation (adaptation). This was the theory championed by F.E. Clements.

3. That species possess a hidden capacity for genetic variability which is selected for when the plant responds to an unusual growth habitat. This was the conventional, neo-Darwinian interpretation championed by Turesson and later experimental taxonomists.

A feature of the debates over the relative merits of these hypotheses was the great conviction with which opinions were held. A striking example of this is seen in F.E. Clements' work. Clements did not die until 1945, long after Turesson's pioneering work on the ecotype concept had become the standard starting point for biosystematical enquiry. Yet, Clements never relinquished his claim that adaptation was the only experimentally verified process discovered in nature to account for the origin of new forms. Neither was this the result purely of Clements ignorance of genetics (cf. Tansley 1946). His discussion of the work of Turesson and Clausen (Clements, Martin and Long 1950: 170, 251) shows that he was familiar with the arguments that were being used against him, but unable to appreciate or unwilling to implement the consequences for his own position.

Can the network model provide a framework for explaining why this was the case? Certainly, if the network model is a naturalistic account of knowledge then it ought to be able to yield insights applied to historical material of this kind.

Consider first a hypothetical example which will be used to illustrate the possibilities of the network model when applied to this kind of data. Imagine a botanist examining a little known flora in a geographical region whose two main ecosystems are meadow and woodland. In the course of his investigations the botanist observes

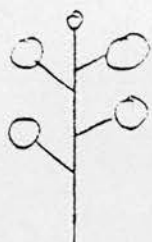
populations of a plant growing in the meadows of this region, populations which for the moment we may designate as "population type A". At a later stage of his investigations the botanist also discovers in the woodland nearby small numbers of plants very similar in overall appearance to A, but with minor, consistent differences in external morphology. Let us call these plants "population B". For our purposes it does not matter very much what the external features which separate A and B are. For the sake of argument we can say that members of population B have a different shape of leaf to population A and that the leaves of B are a darker green in colour. If our imaginary botanist is a taxonomist he may decide that population B merits taxonomic recognition as a variety of A. Indeed let us suppose that this is the case and that the taxonomist calls population A Planta typica and population B Planta typica var. shadensis.

If our botanist were a modern biologist, how would he interpret such a finding in evolutionary terms? A likely hypothesis he would formulate would be that var. shadensis evolved from P. typica as a shade form, in response to the selection pressures of the woodland habitat. If our botanist was a genecologist, the next thing he would want to know was whether or not the variation exhibited in population B was purely a response to environment or whether it was hereditary. How can this be determined?

It is very likely that to test out these two hypotheses our imaginary botanist would conduct transplant experiments in a uniform habitat very like those which Turesson conducted in Sweden in the 1920's. That is he would grow samples of population A and population B in a uniform habitat, where conditions of high light intensity prevailed. If in subsequent generations var. shadensis retained the morphological features which separate it from Planta typica then it would be an ecotype of the latter, in Turesson's original sense of that term. Alternatively, if subsequent generations of var. shadensis grew up as identical with P. typica, then this would be interpreted as showing that the growth habits of var. shadensis in woodland were purely a response to habitat factors, and we would have an ecophene in genecological terminology. These two possibilities are outlined diagrammatically in figure 6.5.

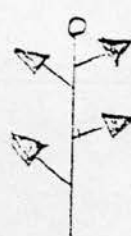
Figure 6.5. A Thought Experiment in Experimental Taxonomy (for explanation see text)

Meadow



Population A
Planta typica

Woodland

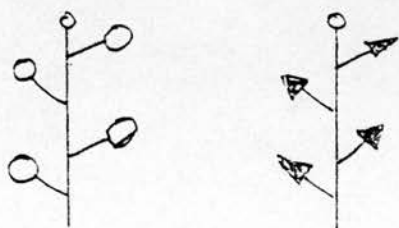


Population B
Planta typica var. shadense

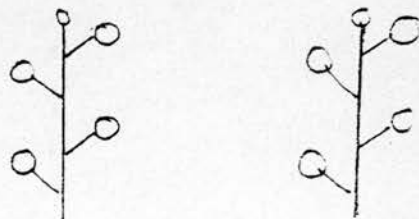
Cultivation under uniform
Conditions with sunlight.

VARIATION IN SUBSEQUENT GENERATIONS

RESULT ONE



RESULT TWO



That then is the kind of interpretation which a modern botanist might well place on the observations he had made. We can call such a botanist a "neo-Turessonian". Now let us try to forget what we "know" about the "facts" of modern biology and try to imagine how a botanist with a theoretical commitment to neo-Lamarckian doctrines of evolution might interpret such data. For the sake of argument, and to demarcate such a botanist from the "neo-Turessonian" genecologist, we can call this botanist a "neo-Clementsian". Would such a botanist be forced to abandon his beliefs in neo-Lamarckianism, given that he made the same observations?

The answer, surely, is that he would not, although the theoretical "gloss" which he would construct to account for such findings would be quite different. To begin with, the neo-Clementsian would challenge the assertion that population A and population B belonged to the same species. He would remind the neo-Turessonian botanist that the term "species" is a notoriously vague one, a hang-over from the pre-scientific era when taxonomy was a herbarium "science". Population A and population B would, from this perspective, represent not two different sub-groups within a species but simply two different "forms" or "adaptants", both of which had evolved from the direct influence of the environment on the plant body (ecogenesis). If, on carrying out transplant experiments, population B maintained its marker characters then the neo-Clementsian would interpret this as proof that the variation caused by the environment in population B had become "fixed". Alternatively, if population B reverted back to type then this would be proof that the fixation stage which follows ecogenesis had not been completed.

So much for the neo-Turessonian and neo-Clementsian. What would happen if a "neo-Lotsyan" joined the discussion? Would his theories be in jeopardy from the observations which had been made? Again, this is surely not the case. A neo-Lotsyan would, though for different reasons than the neo-Clementsian, challenge the neo-Turessonian's initial assumption that population A and population B are members of the same species. Indeed, for the neo-Lotsyan the transplant experiment would itself become a test of this assumption. If population A and B remained distinct in subsequent generations, then this would constitute a proof that A and B were not the same species. Alternatively, if

population B reverted back to type, then this would be a proof that population A and population B were really the same Jordanon and that this fact had been masked by environmental, non-hereditarian influences which had acted upon population B when it was growing in the wild.

The case given above is an imaginary one, although arguments over theory very like this case did take place in the history of experimental taxonomy during the course of the twentieth century. Naturally, the actual development of these arguments in their historical context was immensely more subtle and complicated than this simple example suggests. However, at the very least, this example does help to clarify the problem posed for the historian of science at the beginning of the section. It does show, in a plausible way, the kind of processes which were operating that led a botanist as good as F.E. Clements to reject the refutation of his evolutionary views that was put forward by Turesson, Clausen, and others prior to his death in 1945.

Discussion: Theory change in Science, the Role of "Side-bets" and "Making-out" in the Development of Scientific Culture

We saw in our discussion of the history of experimental taxonomy or biosystematics that there was (and for that matter there still is) no agreed consensus as to what constitutes a species. Given this it is not surprising to find that there are no crucial experiments or definitive observations which can unambiguously settle the question of how species are formed. From the point of view of the network theorist this should not be surprising either. Concepts of how species originate such as "hybridization", "adaptation", "selection" and "ecogenesis" are open-ended and negotiable in the same way that concepts like "whale", "fish" and "mammal" are open-ended and negotiable.

Indeed the present study is far from unique in reaching the present conclusion. An increasing number of studies in the philosophy and history of science have emphasised that theory change in science is problematical and not susceptible to easy and neat "logical" solutions. To take but two examples from this literature, we may consider briefly the work of Toulmin and also of Farley and Geison.

Toulmin (1957, and see also Toulmin and Goodfield 1962: 207-238) has demonstrated that there were no crucial experiments which established the supremacy of Lavoisier's theory of oxygen over its great rival, the phlogiston theory of calcination. Priestly was aware of the experiments which Lavoisier had conducted, but could explain them in terms of the phlogiston theory. In fact, Priestley believed that he had conducted an experiment which provided a crucial test in favour of the phlogiston theory. Toulmin's conclusion is that there is no need in this instance to see Priestley's continued support of the phlogiston theory as an 'irrational' one.

A similar conclusion is reached by Farley and Geison (1974) in their account of the nineteenth-century controversies in France over the question of spontaneous generation. As Farley and Geison show, this controversy was not resolved at the level of experimental fact. Indeed, Pasteur (the leading opponent of abiogenesis) was only able to deny the possibility of spontaneous generation by suppressing part of his own researches. He never found any convincing explanation for the apparent success of some of the experiments to create micro-organisms and his own dislike for the doctrines of spontaneous generation appears to stem as much from religious and political concerns as from purely scientific considerations.

Studies like these, and the present one, raise interesting problems when considered in the light of philosophical accounts concerning scientific rationality. They show that cultural change in science is a non-rational process, if by the term "rationality" we mean what most previous philosophers of science have meant by that term.⁸ Does it follow then, that cultural change in science is a non-rational process? In fact that conclusion does not follow, although in order to save the concept of rationality we shall have to develop it in a manner which is naturalistic rather than normative (for a fuller discussion of the general approach being adopted here see Barnes 1976).

8. For a critical attack on the notions of scientific rationality applied in philosophy of science see Bloor (1971).

To demonstrate the validity of this claim we shall begin by considering the work which has been done in social psychology on the general problem of how and why individuals change and develop their beliefs and life-styles. The relevance of this material to our present concerns will be fully justified later. For the moment let us consider, in particular, the brilliant work which has been done on personal changes in adult life by Howard S. Becker (1964).

The starting point of Becker's work is the realisation that, in accounting for changes in people's behaviour and beliefs, we must seek an explanation not solely in terms of internal changes of "personality" or "values", but in the effects of social structure on the individual's perception of his experience. Thus, as an individual moves in and out of a variety of social situations and interactions, he learns the requirements of continuing in each situation and of achieving success within it. If he has a strong desire to continue, the ability to assess accurately what is required, and to deliver the required performance, becomes a major goal for the individual concerned. Becker describes acting in this manner as situational adjustment or "making-out". Situational adjustment can be used to explain the changes in attitudes and behaviour which actors undergo as they move through the varied social experiences of their adult life.

However, changes in attitude and behaviour, even if they are potentially infinitely plastic and mutable, are rarely developed in this way. Individuals often do show consistency in behaviour which is genuine and not simply a gloss. How can we account for the consistency which we observe in adult development? To account for this phenomenon Becker introduces the related notions of commitment and side-bets. A person is said to be committed, "when we observe him pursuing a consistent line of activity in a sequence of varied situations" (Becker 1964: 49). The process of commitment involves linking extraneous and diverse lines of action towards particular long-term goals. By the very act of living a person normally becomes involved in an increasing number of side-bets - getting a job, getting a car, getting married, having children - which will serve to constrain future behaviour and produce a consistency of lifestyle and belief. The erratic behaviour of the juvenile delinquent, suggests

Becker, may stem precisely from a lack of involvement in situations which commit him more or less permanently to a given line of action.

For Becker then, the change which occurs in any given individual's life-style and belief is a vector, the product of two antagonistic forces. On the one hand there are situational adjustments which necessitate continual change and shifts in behaviour and belief. On the other hand, there are past and current commitments and side-bets which can make such change difficult to achieve. Of what relevance has this to the problems of theory changes in experimental taxonomy during the twentieth century?

To see the relevance consider again the work of F.E. Clements. In Becker's terms Clements had a very strong commitment to neo-Lamarckianism as an explanation for the origin of new species or "forms" in nature. The reasons why this commitment was such a strong one in Clements' work were probably varied and are difficult to precisely locate. In part no doubt the commitment stemmed from the fact that, during the early period of his career, neo-Lamarckianism was a perfectly respectable scientific doctrine, which seemed to explain some of the problems surrounding the origin of species in a much better way than could "neo-Darwinism". In part perhaps, the commitment sprang from an "ecological determinism" which was linked in turn to a strong desire to see ecology become a major discipline within biology. And it is also possible that ideological or political factors played a role in Clements' support of neo-Lamarckian theories of speciation (see Chapter 7). However, whatever the reasons for his continued commitment to these doctrines, the fact of his commitment is beyond dispute. It manifested itself in nearly every paper and article which Clements produced, both in ecology and taxonomy, from his earliest papers until his death in 1945. Indeed, these publications themselves from, in Becker's terminology, side-bets or investments in neo-Lamarckian theory.

Clearly in Clements' case these side-bets and commitments to neo-Lamarckianism made adjustment to the developments which took place in genecology and experimental taxonomy after 1930 very difficult. By 1945 Clements must have been aware that his views were no longer in accord with those of the modern generation of biologists, trained

as they were in the new disciplines of genetics, cytology and synthetic evolution. Clements tried in his later works to make some attempts to adjust to the work which Turesson and Clausen were doing, but the attempts were feeble and lacking in conviction. The result was that by 1953, only eight years after his death, Clements' name was already being written out of the textbooks. Heslop-Harrison in his popular textbook on experimental taxonomy makes only one reference to Clements' work in the text, and that is to dismiss his work for its lack of knowledge of modern genetics and for its lack of awareness of the pitfalls surrounding experimentation with plants (Heslop-Harrison 1953: 22; and see also Heiser 1969: 110). Indeed, in a later publication in which he reviews "forty years of genecology", Heslop-Harrison (1964) does not mention Clements' work at all, he begins his account immediately with a discussion of the work of Göte Turesson.

This interpretation of Clements' later work in experimental taxonomy becomes even more plausible when we consider the later writings of Clements' colleagues and co-author, Harvey Monroe Hall. Hall, like Clements, had made certain commitments to neo-Lamarckianism because in The Phylogenetic Method in Taxonomy, which was the product of their joint authorship, Hall and Clements had interpreted their experimental data in the framework of a neo-Lamarckian theory of "species" evolution. However, unlike Clements, Hall had never previously taken this position with regard to evolutionary questions. His previous work had been either "pure" taxonomy or descriptive phytogeography. In addition Hall, again in contrast to Clements, had connections with Californian biologists, notably E.B. Babcock and his associates at Berkeley, who were strong selectionists. As a result Hall did, in his later publications, firmly repudiate neo-Lamarckian theories of adaptation, even although he died some 13 years before Clements, in 1932.

In retrospect, we might wish to say that Hall was "right" in endorsing natural selection as the major force in speciation and that Clements' theories of ecogenesis and adaptation were "wrong". However, in explaining why Clements and Hall acted in the manner in which they did, such an evaluative stance is neither necessary nor helpful. The action of both men can be accounted for in terms of notions like situational adjustment, commitment and side-bets, in a

manner which is symmetrical with respect to the truth or falsity of the beliefs which they held.

Indeed, Becker's work can be applied not just in dealing with the work of individuals but at the level of whole disciplines or research traditions as well. Consider again orthodox and experimental taxonomy. Experimental taxonomy can be seen as an attempt to "make out" or create a kind of plant taxonomy which would be of value to the needs of twentieth-century biology. Those needs, as interpreted by experimental taxonomists were, as we have seen, to provide a better system of classification for units below the level of the species and to produce classifications which would be genuinely phylogenetic. In the later development of experimental taxonomy these aims become substantively modified, but during the early phase of the disciplines development these were objectives which were shared, even between such otherwise diverse figures as Clements, Turesson and Gregor. These figures were attempting to make a situational adjustment to the needs of biology as it entered the modern period of its development. And, the major commitment or side-bet which had to be made was nothing less than the commitment to an experimental methodology for the discipline of plant taxonomy.

The notions of situational adjustment, commitment and side-bet can also be used to fill out the concept, presented at an earlier point, of interests in technical prediction and control. For situational adjustments, previous side-bets and the like form the "backdrop" against which interests in prediction and control are formulated, modified and sustained. Good science is the art of knowing what you can achieve with the resources at your disposal and when to go about doing it. To succeed in creating a new discipline or sub-discipline the right "tools" (both conceptual and instrumental) have to be available and there has to be a market for the finished product. And this is especially true in a discipline like taxonomy, where the finished product (i.e. classifications) are supposed from the very start to be of service to other pure and applied branches of biology.

Finally, we can return to the starting point of this discussion and consider what should be done with the notion of scientific

rationality. The answer can only be sketched here, but it would seem to us that there is little justification in calling, for example, the actions and beliefs of either Hall or Clements "irrational". Both men were making rational decisions in the light of the situation which was developing in experimental plant taxonomy as they perceived such developments. There are no grounds whatsoever for thinking that either of them was acting in "bad faith" or trying to "fudge" the issues involved. But, the kind of rationality which they were employing is not one that is unique to science or scientists. Actors in all institutionalized systems of action and belief employ this kind of rational decision making (Barnes 1976: 124). The notion of rationality cannot be used, like an axe or a sword, to separate true belief from falsehood, to separate "us" from "them".

Chapter Seven: The Role of Professional Vested Interests and Ideological Concerns in Controversies between Orthodox and Experimental Taxonomists

It will be clear from the material already presented that the introduction of experimental methods in taxonomy was attended by a considerable degree of controversy. The early pioneers of experimental taxonomy such as Clements and Turesson believed they were formulating a new kind of taxonomy which would eventually replace orthodox herbarium methods, and controversy prior to 1930 mainly centred on discussions concerning the validity of this claim. In the 1930's and 40's, as the complexity and diversity of intraspecific patterns of variation became increasingly apparent, this "strong programme" for experimental taxonomy was increasingly abandoned. However, although conflict between the two camps was diminished in the 1930's, it by no means ceased. Highly polemical disputes between orthodox and experimental taxonomists continued to rise after 1930 and have remained a feature of contemporary taxonomic research.

The issues through which these disagreements became manifest were varied. One major facet of dispute revolved around conflict over how best to define species; in effect "species" was a term which both experimental and orthodox taxonomists felt they had a right to claim. A second issue of related concern was that of whether sibling species should be given formal nomenclatural recognition. A third area around which much controversy crystallized after 1930 was the taxonomic treatment of hybrids. And underlying these substantive issues of disagreement has been the wider question of to what extent is it desirable to incorporate experimental and evolutionary data into taxonomy, an issue which, as Rollins (1953) observes, remains unresolved.

How did this controversy, or rather series of controversies arise, and by what mechanisms has such conflict been sustained. In Chapter 6 it was shown that the orthodox and experimental taxonomic communities have different goal orientations or interests. These different interests in technical prediction and control show why the classifications of natural kinds deployed by the two communities are different in their nature. Is it enough to point out different conflicting aims to account for the controversy between the two sides? Or does an understanding of this controversy require an explanation which goes beyond the purely

cognitive aspects of science and makes reference also to professional interests or perhaps even ideological concerns?

The object of this chapter is to examine these questions in the light of a number of recent models which have been presented as general accounts of the nature of scientific controversy. In presenting this material these general accounts will thus be compared with the historical evidence presented in earlier chapters. We shall begin with theories of scientific controversy put forward in positivist accounts of science.

The Positivist Account of Controversy in Science

According to the positivist doctrine science is the only means by which genuine knowledge can be derived.¹ The scientific method, which allows statements to be given empirical meaning, results in the cumulative discovery of more and more pieces of reality or experience. Consonance with reality (or experience) defines the content of science, and the latter consists of genuine knowledge rather than mere belief or prejudice.

On this account the basis for scientific controversy cannot be in knowledge itself - for this is shared - but in incidentals. For example, who discovered a piece of knowledge might be a legitimate source of controversy, but not what was discovered. Controversy does not involve the heart of science for that is a set of statements whose truth has been verified. As an example of a sociologist whose vision of scientific controversy was attuned to this philosophical position we can consider the work of R.K. Merton.

Merton sees conflict in science as a product of competition for recognition (Merton 1957, 1961). Such a desire for recognition on the part of the scientist stems not from individual egocentricity but in response to the institutional patterns of reward manifest in scientific practice. Such an emphasis on recognition and reward led Merton to stress the role of priority disputes in scientific conflict. Priority

1. This doctrine had its origins in the writings of Comte, Mill and Spencer. For an account of these philosophers' ideas see Watson (1895).

disputes are functional because they settle the issue of who really should get recognition for being first to make an important discovery or theoretical advance. However, other forms of scientific controversy are dysfunctional. They violate the norm of Organized Scepticism, the latter being a methodological and institutional mandate that urges:

The suspension of judgement until the facts are at hand and the detached scrutiny of belief in terms of empirical and logical criteria ...

(Merton 1968: 614)

Whatever the final assessment of normative sociology proves to be,² there is no doubt that Merton's account of scientific controversy yields little insight in understanding the conflicts surrounding the use of experimental methods in taxonomy. Priority disputes do occur in taxonomy and the International rules of botanical nomenclature are designed to take account of this fact. However, priority disputes have not been a feature of the disagreements between orthodox and experimental taxonomists. The controversy in this case has been a long and sustained one, often involving violent polemic, and yet disputes have involved not priority claims but (in the first instance) questions of definition, technical practice and differing theoretical and methodological commitments. Nor is there any evidence that these disputes have been abnormal or dysfunctional. Indeed, a fundamental weakness of functional analysis is that it is almost impossible to see how evidence of such "dysfunctionality" could be obtained. Certainly, protagonists in the disputes have sometimes deplored the highly polemical nature of the debate, often as a way of further criticising their opponents position (see, for example, Turrill 1958). However, other taxonomists have argued that the controversy in their discipline is a positively healthy sign, showing a willingness to vigorously debate the relative merits of changes as opposed to simple rejection or acceptance (Rollins 1953). We can never know how taxonomy would have developed if there had been no controversy over the usage of experimental methods. In the absence of such evidence we have only the scientists' opinions and judgements and these cannot be taken at face value, nor indeed are they consistent.

2. For a general discussion of "normative" and "interpretive" approaches to the sociology of science see Law and French (1974).

To summarise: the present case study indicates that organized scepticism although it is sometimes advocated by scientists, is rarely obeyed. Nor is the present case study the only one to demonstrate such a conclusion. Hagstrom (1965) found a similar pattern to be prevalent in the physical sciences:

Whatever the validity of the positivist ideal as a norm - and it is questionable - it is certainly false as a description of the behaviour of scientists. Scientists do become committed to theories for which there is insufficient evidence to convince their colleagues, they do argue strenuously amongst themselves about the validity of opposed theories, and these arguments do become socially structured. There are "schools of thought" in physics as well as the other species. Scientists often act as if they did not accept the positivist ideal or as if its scope were limited.

(Hagstrom 1965: 256)

In conclusion it is tempting to pose the question of why Merton restricted his account of scientific controversy to priority disputes? As has been suggested above the answer to this question would seem to be that Merton held to a naively realistic philosophy of scientific progress. Such a position is implicitly rather than explicitly advocated in Merton's own work, but it is well brought out in the writings of the American philosopher of science Donald Campbell. For Campbell reality forces its conclusions upon the scientist, whatever his own interests and dispositions. The analogy here is with different rats in the same maze. Regardless of the initial starting points the rats will eventually be forced to the same "conclusion". So to with the scientist. Whatever his initial methods and interests he will eventually be forced to discover the same knowledge as his colleagues:

A major empirical achievement of the sociology of science is the evidence of the ubiquity of simultaneous invention. If many scientists are trying variations on the same corpus of current scientific knowledge, and if their trials are being edited by the same external, stable reality, then the selected variants are apt to be similar, the same discovery encountered independently by numerous workers. The process is no more mysterious than that all of a set of blind rats, each starting with quite different patterns of initial responses, learn the same maze pattern, under the maze's common editorship of the varied response repertoires.

(Campbell 1974: 435)

If this view were correct then a sociological account of scientific controversy would indeed be restricted in scope. Sociological explanations would be needed to explain why some scientists irrationally refuse to be "edited" by reality just as presumably, species "psychological" explanations are needed if a rat refuses to learn the correct solution to a maze. However, no explanation would be required for rational correct "science-making". Happily, however, Campbell's quote puts things the wrong way around. Reality does not edit the scientists interests and beliefs. Rather the scientists goals and interests inform and structure the manner in which he organises and "edits" reality. For the rat the maze is a given, independent variable. But, knowledge is not revealed in this fashion, like manna from heaven. And reality is capable of sustaining and supporting many different systems of knowledge and belief.

The failure of positivist accounts of sciences to yield useful insights on the controversy between orthodox and experimental taxonomists suggests that an alternative might be sought from more recent trends in the philosophy and sociology of science. The value of these recent trends is that, in contrast to positivism, they emphasise the problematic nature of cognitive aspects of science. As a consequence the content of science becomes a phenomena worthy of study in its own right. Kuhn's account of scientific growth and change was the seminal influence in directing the attention of historians and sociologists along this pathway.

Kuhn's essential position as outlined in The Structure of Scientific Revolutions is well known and will only be briefly recapitulated here. The most novel insight of Kuhn's analysis is the claim that scientific practitioners are engaged for much of their time in doing "normal science", that is "research firmly based upon one or more past scientific achievements, achievements that some particular scientific community acknowledges for a time as supplying the foundation for its further practice" (Kuhn 1970: 10). These past achievements serve to legitimate and define what constitutes proper explanation and methodology for the science in question but are also open-ended leaving many problems unsolved. The existence of this strong network of shared theoretical, instrumental

and methodological commitments constitutes what Kuhn calls the paradigm of a normal science (Kuhn 1970: 10-12). Paradigms consist of the community's shared system of beliefs and practices and are thus more than simply rules of research.³ In working with a paradigm the scientist tries to make as close fit as possible between the world and the paradigm; normal science is thus a puzzle-solving activity.

In the course of pursuing normal science the scientist will generate anomaly. Some anomaly will be tolerated, but if such anomalies persist in defying resolution and grow in number, the science will enter a crisis state. At this stage anomaly as such will become more generally recognised by the scientists concerned.⁴ More time will be spent on examining fundamental assumptions. More divergent and extreme revisions of theory will be attempted, revisions which at an earlier stage would have been considered illegitimate. Scientific conflict and controversy during such periods will be particularly manifest (Kuhn 1970: 84-91). The resolution of this period of pre-revolutionary science comes when a new paradigm is successfully articulated. However switching paradigms is not an easy matter. Fundamental innovation is resisted. Often it takes a new generation of scientists to carry the day. And, it is only possible to see that a scientific revolution has taken place after the successful emergence of the new paradigm (cf. Kuhn 1962).

Kuhn's view emphasises the scientist's commitment to particular theoretical-methodological traditions (paradigms) and the limits which these impose on radical innovation for most of the time. Scientists holding different paradigms are, in a sense, inhabitants of "different worlds" (Kuhn 1970: 111-135). An important feature of paradigms is their incommensurability. Adherents of different paradigms tend to 'talk through' one another and they will evaluate each others' merits and weaknesses by the different criteria of their own paradigms. Thus,

3. Although it is from paradigms that these rules of research are abstracted and deployed (Kuhn 1970: 43). Thus, one reading of Kuhn's account of science is that it provides cognitive norms to replace the Mertonian norms of organized scepticism, etc. (cf. Mulkey (1969)). However, this is an approach which can be criticised from an interpretist perspective.

4. Kuhn's treatment of anomaly is suspect here. There is no account of why anomaly is tolerated in some periods of a science's development but not others.

for Kuhn, controversy in science can be a result of different communities of scientists holding different paradigms.⁵ The result of such controversy and conflict in the long run is resolution as scientists switch from the old, defeated paradigm to the newly-emerging tradition. However, by the very nature of the context, the making of such a switch is not the logically determined process which previous philosophers of science had imagined it to be. For Kuhn, controversy is an inevitable outcome of different paradigm commitments. As such, it is closely connected to the emergence of new sciences. Controversy is a major mechanism whereby cognitive change in science takes place.

Does Kuhn's account of controversy in science throw light on the controversy between biosystematists and orthodox taxonomists which were described in the earlier chapters of this account? Clearly Kuhn's work does provide some valuable insights. Orthodox and experimental taxonomists share very different instrumental, methodological and (to a lesser extent) theoretical commitments. To the extent that this is the case they can be said to constitute different paradigms sharing communities. In addition, the early experimental taxonomists did often claim that they were out to revolutionise and radically transform the nature of biological classification as a scientific activity. However, although the Kuhnian account of controversy in science can probably fit, at least in part, the controversies which have surrounded the development of experimental taxonomy, there are objections to accepting such an account as a full explanation of the episode.

It might be thought that one problem which arises is that orthodox and experimental taxonomists, although they may have possessed different paradigms, nevertheless shared many background beliefs and assumptions as well. No modern herbarium taxonomist would question either that species evolve or that the species is a genetically and phenotypically complex and heterogenous unit. What they would deny is that cytogenetical

5. The relationship between the concepts of 'paradigm' and 'scientific community' is dealt with in the postscript to the 1969 edition of S.S.R.

and evolutionary evidence can always be usefully incorporated into formal plant classifications. However, in spite of the claim of Darden (1976), this is not a devastating criticism of Kuhn's position.⁶ We should expect scientists, even scientists who are members of different paradigmatic research traditions, often to share many background assumptions and beliefs.

A more serious discrepancy is the fact that the controversies between orthodox and experimental taxonomists appear to have been engendered in a context which bears little resemblance to Kuhn's characterisation of science in a crisis or pre-revolutionary state. The legacy passed on to herbarium taxonomy at the start of the century was that of describing and ordering, by means of monographs and floras, the vast diversity of plant species found on the earth. In spite of the claims sometimes made to the contrary by experimentalists (e.g. Heslop-Harrison 1953: 10), this objective is still nowhere near completion.⁷ In carrying out this task there has been no crisis of methodology or revolution, the methods employed are still largely those developed in the 18th and 19th centuries, notably herbarium analysis based primarily upon external morphology. And for much of this work experimental methods are not suitable, as some experimentalists have themselves admitted (e.g. Hall and Clements 1923: 1; Clausen 1931: 303; Gregor 1939; Keck 1959).

It is clear that orthodox and experimental taxonomy do represent, in some sense, different paradigms or research traditions within taxonomy. And, there is formal incommensurability between the classifications which are produced when either mode of approach is adopted. To take just one of the examples discussed in the last chapter, Gilia inconspicua cannot be both a single species and five

6. Darden argues that Darwin and De Vries shared many assumptions in their scientific work, although they possessed different "paradigms" in Kuhn's terminology.

7. It has been estimated that of the 10 million or so species in existence only some 10-15% have been described by taxonomists (see Raven, Berlin and Breedlove 1971: 1210).

different species. However incommensurability is not, in itself, an explanation for why controversy has existed between the two disciplines. It would have been quite possible for orthodox and experimental taxonomy to have been regarded as mutually complementary approaches to the study of biological natural kinds and indeed, such an approach is advocated in some of the more recent taxonomical literature (e.g. Raven 1974). Cognitive factors alone do not explain why conflict occurs because conflict itself is a choice rather than a matter of any logical necessity:

Theorists can happily maintain opposing views in a state of peaceful coexistence as long as such theories remain inconsequential for group practice. Whenever professional or political interests are at stake, however, theoretical differences are transformed into heated controversy and elements of the intellectual substance of those theories will mirror threatened interests.

(Harwood 1979, 232)

To summarise: Merton's account of controversy in science possesses the merit of emphasising science as a social activity and conflict as something which arises out of the social and institutional structure of scientific patterns of interest and reward. However, Merton restricted his account of scientific controversy to priority disputes. As a result, controversy in science becomes something which is peripheral, which takes place after a scientific discovery has been made. Kuhn's work removes this anomaly and places conflict and competition in science at the heart of enterprise - within scientific cognition. However, the weakness of this approach is that it does not give cognitive disagreements in science a satisfactory basis in institutional organization. Why should different groups take opposed technical positions?

Different cognitive interests (or interests in prediction and control) are a necessary but not sufficient condition for controversy to occur. To explain the controversy between orthodox and experimental taxonomists we must examine Harwood's "professional and political interests" and their respective roles in the material presented in earlier chapters.

Professional Vested Interests as an Explanation of the controversy
between Orthodox and Experimental Taxonomists

Biologists in the twentieth century have become increasingly experimental in their aim and outlook. As Garland Allen has observed:

Contemporary biology is ... marked by a highly experimental viewpoint. The twentieth century has witnessed the continuous attempt of biologists to bring their fields of endeavour within the rigorous domains of experimental analysis ... Modern biologists have demanded more than observation and description of organisms or their processes. This demand is for the methods of experimental analysis and the attempt to study biological processes on a number of levels, chief of which has been the level of molecular interaction.

(Allen 1975: xiv-xv)

The change from observation and description to experimental analysis was more than just a matter of methodology. It also involved a change in the type of explanations considered appropriate in biological investigation. The biologists of the new experimental school were concerned with locating causes of biological phenomena, often in microstructure. Analogues with chemistry and physics were commonly made, and many adherents of the "New Botany" of the 1880's were mechanists in their approach to plants, holding that the proper explanation of biological phenomena lay in their chemical and physical make up.

To begin with the use of the new experimental methods was confined mostly to physiology. It was also a movement which in the nineteenth century was especially prominent in Germany. However, the spread of experimental methods from German physiology to other countries and other disciplines of biology was well under way by the turn of the century,

The spread of experimental methods from physiology to previously more descriptive areas came first in embryology in the 1880's with the rise of the "developmental mechanics" of Wilhelm Roux (1850-1924) ... From embryology the experimental approach spread to cytology and heredity, and finally to evolutionary theory. Each instance saw a transformation of the kinds of questions being asked and the kinds of methods used to answer those questions, from descriptive and speculative to experimental and quantitative. By the 1930's most areas of biology, except perhaps paleontology and systematics, were loudly claiming new advances because of the use of experimental analysis and the methods of physics and chemistry.

(Allen 1975: xvii)

Seen in this light the attempt to introduce experimental methods into plant geography (ecology) and systematics (experimental taxonomy) were part of a much wider movement to experimentalise and quantify all forms of biological enquiry. The revolt from morphology evident in the writings of experimental taxonomists in the 1920's was part of a general trend away from morphology, and a trend which united such otherwise diverse biologists as Bateson, Weldon, Morgan, Clements, Turesson, Lotsy and De Vries.

In both ecology and taxonomy the use of experimental and quantitative techniques was linked to professional objectives and goals. These concerns are especially manifest in Clements writings. Clements believed that amateurs would have to be excluded from ecology if the status of the discipline was not to be damaged:

No subject has suffered more from the lack of training and experiment or from the absence of basic procedure and adequate perspective. It has become obvious that this condition can be remedied and actual progress insured only by instrumental and experimental methods and by a combination of intensive and extensive studies that will check superficiality on the one hand and broaden limited horizons on the other. It is certain that much work of purely superficial or local character will continue to be done under the name of ecology, but the touchstones of instrument, quadrant, and experiment afford a ready means of eliminating such papers from consideration. No study deserves to be called ecological that does not deal with the cause-and-effect relation of habitat and organism in a quantitative and objective manner.

(Clements and Weaver 1924: 3)

And within taxonomy experimental and quantitative techniques have continued to be justified on these grounds. According to Sokal and Sneath taxonomy is handicapped by the inadequate training and background of many of its participants:

It is surely a reflection of the state of the science that the description and classification of organisms is today one of the few fields of biology to which amateurs without sound theoretical and practical training are able to contribute ... As more sophisticated ideas and techniques percolate through systematics, amateurs not trained in modern taxonomy will find their sphere of activity progressively more circumscribed.

(Sokal and Sneath 1963: 9-10)

One consequence of the triumph of experimentalism in twentieth century biology was that systematics of the more descriptive kind came to be seen as having a low status and of being, in effect, an amateur's discipline. Many experimental biologists could see little value or purpose in orthodox taxonomy which appeared to be an activity more akin to collecting postage-stamps than to proper science. Mayr, writing in 1942, recorded this decline in the status of systematics in the following terms:

The rise of genetics during the first thirty years of this century had a rather infortunate effect on the prestige of systematics. The spectacular success of experimental work in unravelling the principles of inheritance and the obvious applicability of these results in explaining evolution have tended to push systematics into the background. There was a tendency among laboratory workers to think rather contemptuously of the museum man, who spent his time counting hairs and drawing bristles, and whose aim seemed to be merely the correct naming of his specimens.

(Mayr 1942: 3)

Experimental taxonomists held out the promise of being able to reverse this trend. In effect the experimentalists sought to redefine and renegotiate the scope of traditional taxonomic enquiry. The new systematist not only employed experimental methods in plant classification, he also was concerned with plant taxa as biological phenomena, with their origins, relationship and biological organisation (cf. Mayr 1942: 11). As a result taxonomy would become once again at the centre of biological research. Babcock saw adoption of such methods as "the only way to get taxonomy the fundamental place it deserves in biology" (1947: 31). Similarly, Turrill, at the end of his paper on "Taxonomy and Genetics", expressed the hope that:

If my remarks do something to remove the common misconception that taxonomy is merely a dry museum or herbarium study, hidebound by tradition, and limited to the preparation of technical descriptions, identification of specimens, and problems of nomenclature, they will achieve an important function. If, further, they serve to attract some younger biologists to studies helping directly towards an "omega" taxonomy they will have fulfilled their main purpose. It remains a fact that taxonomy is now in an interesting condition, and one does not really know what it may bring forth.

(Turrill 1938: 39)

Thus, for orthodox taxonomists, experimental methods held out both a promise and a threat. The promise was that experimental methods would make taxonomy relevant to the needs of biologists in other disciplines. As Lincoln Constance put it in his opening address to the American Association of Plant Taxonomists, the adoption of the new techniques would make it "unthinkable for a department of botany to attempt to get along without a systematist" (Constance 1951: 231). However, the new methods were also a threat to established taxonomic practice. Taxonomists who saw this threat emphasised traditional professional boundaries. Rydberg (1926) did not believe that ecologists could tell taxonomists how classification should be achieved. Bremekamp (1939) made it clear that using experimental techniques involved work which was outside the "domain" of taxonomic enquiry. And even taxonomists who did use experimental methods (e.g. Turrill and Keck) emphasised that much basic research still needed to be done which would utilise the non-experimental approach of the herbarium taxonomist.

In many important ways the emergence of experimental taxonomy at the turn of the century has striking parallels with the birth of psychology in Germany in the 19th century. As Ben-David and Collins (1966) have shown, an important factor in the development of psychology was role-hybridization. Role hybridization occurs when scientists move from one scientific discipline to another and attempt to deploy the methods and techniques of the old discipline to the new one, thereby self-consciously creating a new role. Role hybridization is, therefore, one form of situational adjustment (see Chapter 6). For role hybridization to occur three factors must be present (Ben -David and Collins 1966: 465).

1. The old and new disciplines must both be established with a professional base and thus allow for academic rather than amateur roles to be established.

2. Intellectual migration must be taking place from a discipline or disciplines whose status or academic standing is high to one whose status or academic standing is relatively low.

3. A better competitive situation must be present in the low status discipline, making migration attractive in spite of the more

lowly standing of the discipline into which migration is taking place.

The result when these three factors are present is the formation of a new distinct discipline which uses the methods of the high status fields from which migration has occurred to tackle the problems of aims of the low status discipline in a new and different way. Thus, psychology arose because experimental scientists (physiologists) migrated into philosophy and applied to the latter experimental, as opposed to philosophical, methods. Experimental taxonomy arose in a similar fashion: migrating scientists from experimental disciplines (genetics, cytology and ecology) applied the methods learned in these disciplines to solve problems of plant classification which had, hitherto, been approached from a morphological and descriptive perspective. Clearly this migration also involved movement of scientists from a field with a relatively high academic standing or status to a field with a low and declining standing. What is less clear in the present study is whether this mobility was caused by the existence of a better competitive situation in taxonomy vis-a-vis ecology, genetics and cytology. It is possible that it was not. However, to decide this point one way or the other is not possible at this time. It would require a detailed analysis of institutional location, sources of patronage and degree of scientific mobility which has been beyond the scope of the present investigations. As was stated in the introduction, no work of this nature has been done on twentieth century plant taxonomy and its related disciplines.

What is not in doubt, however, is that professional matters - that is matters of status, image, questions of training and reward - played a key role in the rhetoric of the debate between orthodox and experimental taxonomists. And these professional interests and concerns were closely allied with the different instrumental interests of the two kinds of taxonomy discussed in Chapter 6. For these instrumental judgements are a reflection of the social interests of groups of practitioners with different technical competences and skills. The point here is a general one: because the construction of scientific knowledge is a social process, social and cognitive factors will always overlap and combine in this manner.

That this is the case has some important consequences for historical and sociological studies of science. That scientists are concerned over factors such as status, pedagogy and image should not be seen as an unexpected discovery. Their existence is only made invisible when the history of science is regarded entirely in terms of a history of ideas. However, such factors are also not properly seen as being in any way "external" to science. Such factors will always be present in the emergence of any piece of scientific knowledge and in the growth of all forms of scientific culture, although, of course, their nature and degree of significance in any single concrete instance is a matter of empirical investigation. Their study, therefore comprises what amounts to a previously "hidden" internal component of the history of science.

Thus far then we have analysed the differences between orthodox and experimental taxonomy in a manner which lays emphasis on "internal" factors in the growth of scientific knowledge. For the sake of exposition these internal factors were classified as being interests of two different kinds: interests in technical prediction and control (cognitive interests) and professional vested interests. In practice these two sets of interests are combined in the construction of any given piece of scientific knowledge. What of the role of "external" or wider social interests? Whether interests of this nature shed light upon the differences between orthodox and experimental taxonomy will be discussed in the next section.

The Role of External Factors in the Controversies over Experimental Taxonomy

That social, political and ideological factors of a kind usually considered as "external" to science can sometimes play a role in scientific conflicts and controversies is now beyond doubt. A number of case studies now verify that this is the case.⁸ As one example from this growing literature we can consider the work of Mackenzie and Barnes (1975) on the controversy between the biometricians and the mendelians.

8. Only a small proportion of this literature is considered below. For more examples see Mulkay (1979).

The major "scientific" issue in this debate concerned the nature of the variation through which speciation took place. The biometricians, of whom Karl Pearson was the leading advocate in Britain, held that evolution took place solely by the action of selection on small continuous differences within populations, differences which occurred at the extreme ends of any given characters normal distribution. For the mendelians, and especially for the leading mendelian of this period, William Bateson, evolution took place primarily through saltations or large-scale mutations and hence involved an element of unpredictability not easily susceptible to rigid mathematical analysis. The controversy had, of course, many other ramifications but this was the central point at issue (cf. Provine 1970: 1-24).

Mackenzie and Barnes see this controversy, especially as evident in the writings of the two major protagonists Bateson and Pearson, as intimately linked to the growth of the eugenics movement in Britain during the period from 1890 to 1914. The eugenic programme could be demonstrated as feasible only if evolution was a predictable process susceptible to mathematical analysis. Pearson was an active supporter of eugenics and the reformist and interventionist politics which such a programme of action would entail. Biometry, as developed by Pearson and his colleagues, was designed to provide the theoretical and practical basis for a eugenic position. Eugenacists emphasised the importance of professional-scientific skills in the management of society. Pearson was a typical representative of the new professional middle-class whose interests eugenical reform was designed chiefly to serve (Mackenzie 1976). Bateson, on the other hand, was a conservative thinker opposed to the radical reforms of the new middle classes including eugenical reforms (Mackenzie and Barnes, 1975). For Bateson the chief source for progress, both in science and society lay in the existence of occasional novelty and genius, genius whose importance should be recognised and cultivated but which could not be reproduced as it were 'on demand'. Thus for both figures there are explicit links to be made between scientific beliefs and political, social and ideological interests which are normally seen as external to science.

An important analytical tool in this type of approach to history

of science is the concept of 'styles of thought' first developed by the German sociologist Karl Mannheim (1936). The use of this concept is predicated on the notion of knowledge as the product of man as a 'social animal'. In Mannheim's own words, "it is not men in general who think, or even isolated individuals who do thinking but men in certain groups who have developed a particular style of thought in an endless series of responses to certain typical situations characterizing their common position" (1936: 2-3). Thus for Mannheim a style of thought can be understood as, "a set of concepts linked together by a coherent Weltanschauung" - and also as "a specific approach to reality which tends to influence the method of thinking and the presentation of the facts" (Mannheim 1953: 165).

The most celebrated example of the use of such an analysis is Mannheim's own interpretation of the development of conservative styles of thought in Germany during the nineteenth century (Mannheim 1953: 74-164). According to Mannheim, this style of thinking developed as a conscious repudiation of the "natural law" philosophy of the Enlightenment. The chief characteristics of this mode of thought is its stress on the highly rationalistic, scientific and progressive nature of knowledge. It is also characteristically a mechanistic style of thought. Wholes (be they of a physical, biological or social system) are seen as analysable into their constituent elements or atoms without distortion or error. The whole is the sum of its parts and can best be explained by reduction to its constituent parts.

Conservative thought was a counter-movement which is essentially traditionalist and opposed to the progressive orientation of natural law thinking. Conservative thinkers stressed the concrete and the practical as against the universal and the abstract. The importance of time and historical explanation is often especially emphasised in conservative thought. There is often stress on intuitive and irrationalist forms of methodology and on the failure of general and 'universal' explanations to deal with that which is unusual and unique. The whole is seen as more than the sum of its parts and as not reducible to its atomistic constituents; conservative thinking is holistic and anti-reductionist.

Styles of thought are reactions to specific political, social and intellectual circumstances and the tendency to conceive of them as archetypal or Platonic entities is to be restricted. Nevertheless, the analysis of conservative and natural law thought given by Mannheim does appear to yield insights when applied to other bodies of knowledge in other epochs. Also, in spite of Mannheim's belief that scientific knowledge should be exempted from sociological enquiry, these styles of thought do appear to be useful tools in understanding some controversies within Science (Mannheim 1936: 38-39, 244, 268).

Thus, Harwood (1976, 1977) has found Mannheim's categories of conservative and natural law thought to be illuminating when applied to modern debates over race and I.Q. He suggests that, "contemporary hereditarianism is an expression at the level of scientific theory of its proponents' classic liberal world-view" (1977: 10).

A second use of Mannheim's category of conservative thought is found in Coleman's work of William Bateson (Coleman 1970). Coleman's argument is that it was Bateson's conservatism which explains his initial rejection of the chromosome theory of heredity proposed by Morgan and others in the period from 1900 to 1920. Indeed styles of thought can be used to explain not only controversies within science but also controversies about the nature of science. For example, the long and bitter dispute between Kuhn and Popper is explicable in these terms (Bloor 1976: 48-73). Social and political beliefs it would appear, influence not only positions taken within science but our very conception of the nature of science as an activity.

It is clearly possible that an approach such as this might explain the controversies between orthodox and experimental taxonomists. Stress on the importance of classification as an activity has sometimes been associated with an enlightenment view of science. Gillispie has described opposition to the Linnaean system as "a touchstone of romantic and metamorphic (or stoicizing) tendencies in taxonomy" (Gillispie 1962: 280). Thus, Linnaean botany was one of the major casualties when Jacobin philosophy of science became dominant in France during the period immediately following the French revolution. However, in the twentieth

century the major criticisms levelled against taxonomists have been that they are too "conservative", and traditional in their scientific philosophy. And in attempting rebuttals to this claim, taxonomists occasionally use a language which reveals wider concerns with what are seen as overly liberal and progressive trends in our current societies value-orientations. For example, the zoological systematist Crowson writes that:

If systematics is eventually restored to its central position in academic botany and zoology, this will be one manifestation of a change in the general 'intellectual climate'. Other signs of such a change will be the official recognition of natural history as an aspect of science entitled to parity of esteem with natural philosophy, and the reinstatement of the view that a prime function of universities is the preservation and transmission of a vast heritage of culture and knowledge. Much more effort will be made to inculcate in the young a profound respect for their cultural heritage and correspondingly less emphasis placed on the cleverness of the present. Instead of being taught to despise or patronise previous generations, students would be made to feel that only by tremendous efforts could they hope to match the achievements of their predecessors.

(Crowson 1970: 305)

Can we go further than this and see taxonomy in general as a body of knowledge which has been designed to legitimate and serve conservative social interests and beliefs? In fact, it seems almost certain that we cannot make such an inference. The problems here are two-fold. Firstly, there is no evidence that taxonomists as a body of individuals are proportionately more conservative in their social and political views than other scientists. Such evidence has not, of course, been sought but in its absence there is no positive ground for taking the position just outlined above. Secondly, and of even greater significance, is the fact that taxonomists rarely link their role as scientists with any wider concerns of a political or socio-political nature. Crowson is one of the very few possible exceptions to this statement and even here the case is arguable. Does Crowson want a return to traditional values for their own sake or because he considers that the return to such values would aid taxonomy? And it is worth also noting that even if a conservative "style of thought" is provisionally accepted as being

applicable to some taxonomists this would still not necessarily have any value in explaining the controversy within taxonomy over the use of experimental methods. Crowson is an interesting case in point here, for in spite of his emphasis on the importance of tradition he is a firm advocate of the use of experimental methods in taxonomy (Crowson 1970: 145).

The above observations do not rule out the possibility that ideological concerns were manifest in the writings of scientists considered in earlier chapters. One figure whose work might be particularly rewarding to study from this perspective is F.C. Clements. Duff (1975) has argued that Clement's organismic theory of vegetation development is explicable in Mannheim's categories as a manifestation of conservative thinking. And this observation is consistent with Clement's insistence that classifications of plants should reflect evolutionary history. However, this explanation, if correct, applies only to Clements. It does not provide any evidence that ideological objectives were a systematic source of controversy between orthodox and experimental taxonomists.

In conclusion then, the controversy between orthodox and Experimental taxonomists appears to be one which is largely explicable in terms of 'internal' factors. However, this is a purely empirical finding and one which might be overturned by future investigations. Scientific taxonomies, and by implication other forms of scientific knowledge, are conventional in character. Because of this there are no compelling a priori grounds for denying the possibility that external factors play a role in science. In the future, naturalistic studies of science, whether they invoke "internal" (cognitive and professional) or "external" (political and ideological) interests to account for the growth of scientific beliefs, can be confidently freed from the over-restrictive doctrines of metaphysical realism and essentialism. The sociology of science can never be merely the sociology of error for, as the present study has indicated, those very notions of "error" and "truth" are socially manipulated and sustained.

Appendix A: Numerical Taxonomy and its Significance to a Naturalistic Account of Classification

The 1960's saw the advent of computers as aids to taxonomic investigations, both in zoology and botany. However, this period has seen more than just the use of computers for information, storage and retrieval. It has also seen the emergence of a new approach to systematics, centred on the use of computers and possessing its own philosophy and theory of classification as well. Most of the work in this field has been done in the United States; Sokal and Sneath (1963) have been two of the major advocates.

The main theoretical tenet of numerical taxonomy is that biological classifications should be phenetic, that is based on overall resemblance and that for this reason characters should be weighed equally when a classification is produced. Michel Adanson, the eighteenth century Parisian botanist, held a position similar to this so that numerical taxonomy is sometimes referred to as "neo-Adansonian" taxonomy.

Computers are employed in numerical taxonomy to prevent the, perhaps unintentional, weighting of characters which will occur when classifications are constructed in the normal way. Numerical taxonomists claim that, by avoiding such "subjective bias", numerical techniques provide a more objective classification than that which is possible by other methods.

The production of numerical classifications involves five basic steps (see Sneath 1962 and also Davis and Heywood 1963: 132-137):

1. The first procedure is to select the group of organisms to be studied. These will usually be individuals, either treated as such or taken as representatives of named taxa (normally species). The taxonomic entities to be employed in the classification are termed as operational taxonomic units (O.T.U.'s).

2. As many characters as possible are now found and scored for each O.T.U. In the simplest case, which is all that need concern us here, each character is scored as either present (+), absent (-) or

as not applicable for the O.T.U. in question (N.C.). The result, when each character is scored is a coded data table (t x n table). An example of such a table is shown in figure A.1 for 12 characters and 4 O.T.U.'s. In practice, of course, many more characters would be employed than this, but this can be ignored for illustrative purposes.

3. The third step, having fed the information from the coded data table into a computer, requires calculating a figure which will act as a measure of resemblance for each pair of O.T.U.'s. This is done by means of a coefficient of resemblance. In the simplest case this will consist of a numerical index of similarity (S), such as the following:

$$S = \frac{N_S}{N_S + N_d} \times 100$$

where N_S = the number of positive characters shared in common by any two O.T.U.'s, and N_d = the number of features positive in one O.T.U. but negative in the other.

The result of these calculations is a similarity matrix (t x t table) like the one shown in figure A.2.

4. The O.T.U.'s can now be arranged in a way which brings together those pairs with the highest degree of similarity. This stage of numerical procedures is termed cluster analysis. The simplest way of performing this operation is to take the similarity matrix and shade in the figures in a way which indicates ranges of similarity. The table can then be re-arranged accordingly. This process is illustrated diagrammatically in figure A.3, for a similarity matrix consisting of 10 O.T.U.'s.

5. Finally, the information given by cluster analysis is used to construct a dendogram. The dendogram for the 10 O.T.U.'s shown in figure A.3 is shown below in figure A.4.

From this dendogram it is possible to derive the phenons which are the actual units of numerical taxonomy. What these groups include will depend on the level of the phenon employed. For example, the 10 O.T.U.'s shown in figure A.4 can be arranged in a 3-fold hierarchy representing,

Taxa (O.T.U.s)

character states	A	B	C	D
1	+	+	-	N.C.
2	+	+	+	+
3	+	+	+	-
4	-	+	N.C.	N.C.
5	+	+	+	+
6	+	+	-	+
7	+	+	-	N.C.
8	N.C.	-	+	+
9	+	+	+	+
10	+	+	+	-
11	+	N.C.	+	N.C.
12	+	-	+	-

Figure A.1. Coded Data Table
(from Sneath 1962:112)

Taxa (O.T.U.s)

		A	B	C	D
Taxa (O.T.U.s.)	A	100			
	B	90	100		
	C	60	60	100	
	D	57	50	50	100

Figure A.2. Similarity Matrix
(from Sneath 1962:112)

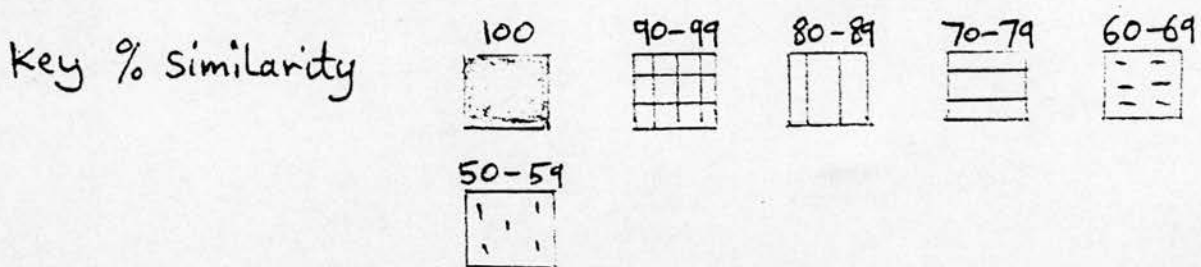
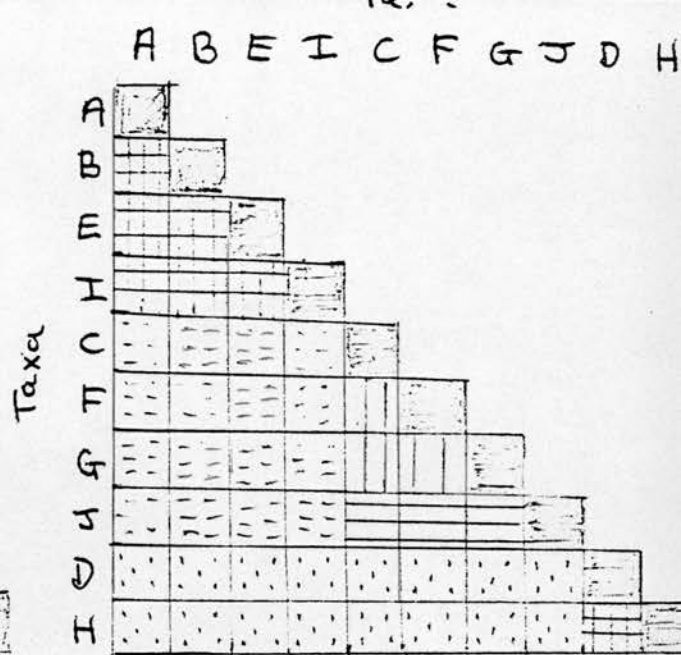
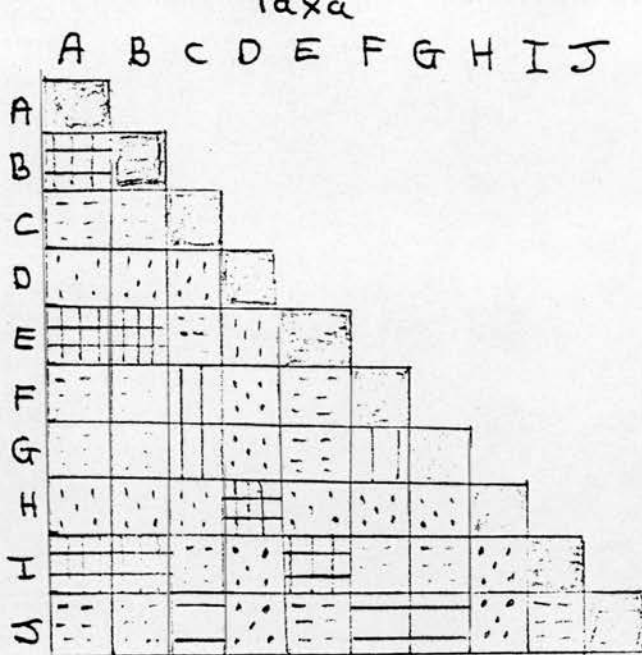


Figure A.3. Cluster Analysis (from Sneath 1962: 113)

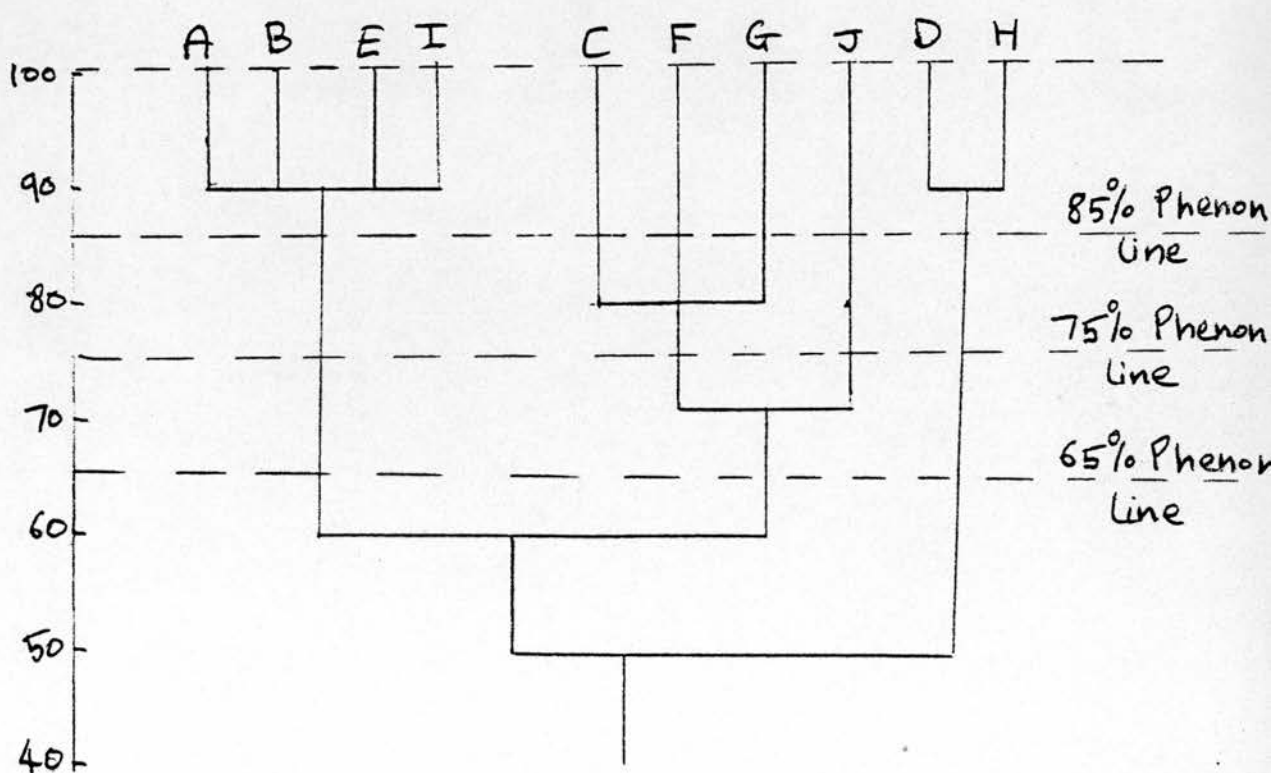


Figure A.4. Dendrogram (from Sneath 1962: 113)

respectively, 85%, 75% and 65% similarity. At the 85-phenon there are 6 groups (ABEI, C, F, G, J, DH). At the 75-phenon there are 4 groups (ABEI, CFG, J, DH). At the 65-phenon level there are 3 groups (ABEI, CFGJ, DH). If desired these phenons can be regarded as species, subgenera, genera, etc. depending on the ranks of the original O.T.U.'s employed in the study. However, there is of course, no necessity to equate phenons with the taxonomic groupings of orthodox taxonomy in this fashion.

The Significance of a Numerical Taxonomy to a Naturalistic Account of Classification

As was stated above, the advantage of numerical taxonomy (or its claimed advantage) is that it delimits groups according to agreed (but arbitrary) levels of similarity which are "objectively" measured. The result is a phenetic classification free from the conscious or unconscious weighting of characters which will occur when conventional methods are employed. It is not appropriate here to discuss the value of such methods to biological systematics or to discuss their likely future impact, although it is worth noting that both these questions have engendered heated controversy. What will be considered here is the significance of numerical taxonomy to a naturalistic theory of classification.

The taxa (or phenons) of numerical taxonomy are polythetic, i.e. definable only by using a cluster of characters. As Sneath and Sokal (1962: 14) put it, "no single attribute is in theory sufficient and necessary for membership in the group so long as the members share a high proportion of characters". And as Hesse (1974: 48) points out, the existence of classifications of this sort in science in itself constitutes a refutation of the claim often made by philosophers that Wittgenstein's family resemblance theory of universals contains logical inconsistencies and circularities.

However, the significance of numerical taxonomy to our account of classification goes further than this. For not only do computers programmed by numerical taxonomists produce polythetic taxa, the methods by which these taxa are produced are identical to the classification theory discussed in chapter two as 'logicalized cluster

description theory'. For the computer a given phenon (P) contains an O.T.U. if and only if that O.T.U. possesses a sufficient number of the cluster of characters used to define that phenon. No character is more important or essential than any other, all characters are weighed equally.

Do humans classify in a manner which is analogous to the computer's functionings? The answer is almost certainly that they do not; indeed this is why computers were introduced. A major dissimilarity centres around the problem of character definition. This is no problem for the computer since what constitutes a character is defined for it by its human operator. However, when human beings undertake a classification there is good evidence that they do so on the basis of a gestalt of often un verbalized perceptions of similarity and difference:

In assessing similarity the taxonomist working neurally does not have to make consciously the abstractions we call characters: it is only when he wishes to communicate about any particular aspect, e.g. for diagnosis, that he is forced to rationalize what he recognises as a gestalt of many independently varying elements, and break it down into component parts. As a consequence of this the taxonomist may produce a satisfactory division into species despite the characters set down in his descriptions.

(Davis and Heywood 1963: 139)

Moreover, the equal weighting of characters is itself a choice. Indeed it is a choice that many taxonomists see as a poor one. If the units formed are regarded as species then the groups so formed may not correlate with genetic and crossability evidence derived from studies of the same populations. Also, the lack of weighting may result in groups where convergence and parallelism mean that the resulting classification conflicts with evolutionary evidence (e.g. in the fossil record). Finally, the species formed in numerical taxonomy may have no single morphological attribute which can be used to separate them from neighbouring populations, making recognition in the field and herbarium an exceedingly difficult task. For these reasons there are many who would question the value of the numerical techniques outlined above.

It would seem then that 'logicalized cluster description theory' describes one strategy for classifying natural kinds. It is not a strategy with which many taxonomists would find favour, although it is a strategy which is particularly well exemplified in the procedures of numerical taxonomy.

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Addendum : Some works on botanical classification not discussed in the text

Beckner, M. (1959), The Biological Way of Thought, New York.

Beckner's book is an attempt, in its author's words, to "investigate the logical features that are characteristic of the biological way of thinking". The chapter on systematics is sympathetic to the claims of the "new systematists", especially Dobzhansky and Mayr. The book was important in persuading philosophers of the existence of polythetic concepts in biology.

Daudin, H. (1926a), De Linné à Jussieu. Méthodes de la classification et idée de série en botanique et en zoologie (1740-1790), Paris.

Daudin, H. (1926b), Cuvier et Lamarck. Les classes zoologiques et l'idée de série animale, Paris.

Daudin's two works are the standard historical reference on biological taxonomy in the period before Darwin.

Gould, S.J. (1979), "Species are not Specious", New Scientist 83 : 374-377.

This paper is a continuation of the old debate over the reality (or otherwise) of species. Gould argues, citing evidence from the anthropological work of Berlin and Bulmer, that species are realities of nature rather than mental fictions of the taxonomist's mind.

Hull, D. (1970), "Contemporary Systematic Philosophies", Annual Review of Ecology and Systematics 1 : 19-54.

Hull's article provides a comprehensive review of the literature in the philosophy of biology on the arguments between phylogeneticists and pheneticists.

Jardine, N. (1969), "A logical basis for biological classification", Systematic Zoology 18 : 37-52.

Jardine uses set theory to formulate a model of how a hierarchic classification works. The aim is to provide an underlying logic for the use of numerical methods in taxonomy. An important aspect of this model is that it does not include an account of the way in which the meanings of taxa are to be specified, so that it avoids the controversies over the meaning of natural kind terms which are dealt with in the thesis.

Levin, D.A. (1979), "The Nature of Plant Species", Science 204 : 381-384.

This is a modern defence of the idea that species are mental fictions rather than realities of nature (c.f. Gould, op.cit.).

- Ospovat, D. (1978), "Perfect adaptation and teleological explanation : approaches to the problem of the history of life in the mid-nineteenth century", Studies in the History of Biology 2 : 33-56.
- Ospovat describes a pre-Darwinian controversy in biology over the use of non-teleological explanations and laws in the life sciences. The paper is relevant because it provides a good example of a scientific controversy in which vested professional interests played an important role.
- Pratt, V. (1972), "Numerical Taxonomy", Journal of Theoretical Biology 36:581-592.
- Pratt argues that there are great difficulties in determining what constitutes a character of an individual organism. This is a major criticism against the use of numerical methods in taxonomy, since in these procedures characters have to be explicitly stated before a classification can be made.
- Pratt, V. (1972), "Biological classification", British Journal for the Philosophy of Science 23 : 305-327.
- Pratt argues that the purpose of biological taxonomists should be to form groups of taxa which allow reliable generalisations from facts established in connection with a few individuals to be made about less well-known taxa of the group. In practice this means our classifications should be phylogenetic.
- Pratt, V. (1977), "Foucault and the history of classification theory", Studies in the History and Philosophy of Science 8 : 163-171.
- Pratt, following Foucault, argues that classical taxonomists, such as Adanson, had a notion of "character" that was finite. This is in marked contrast to the modern view that the number of characters possessed by an organism is (potentially at least) infinite. If Pratt's thesis is historically correct, then the concept of "character" has undergone a radical change of meaning in systematics since the eighteenth century, and this has implications for the claim that numerical taxonomy is "neo-Adansonian".
- Sloan, P. (1972), "John Locke, John Ray and the problem of the Natural System", Journal of the History of Biology 5 : 1-53.
- Sloan's paper is an elegant study of a long-standing argument in taxonomy between those who argued that a natural system of classification should be based upon a few essential characters, and those who argued that a natural system must be based upon overall resemblances of form. The material is of interest because this controversy has parallels with the much more recent

controversies in philosophy between adherents of description theory, like Searle, and essentialists, like Putnam.

Walters, S.M. (1961), "The Shaping of Angiosperm Taxonomy", New Phytologist 60:74-8

Walters claims that angiosperm classification can only be understood in relation to its development in a particular historical and philosophical context, - that of seventeenth and eighteenth century Europe. It follows that our classification of angiosperm families and genera would have been very different if, for example, botanical systematics had developed first in the tropics or southern hemisphere. The general position taken, i.e. that classifications are cultural phenomena that reflect the social aspirations and resources of their creators, is fully consistent with the model of classification presented in the thesis.